

Environmental Hypotheses of Hominin Evolution

RICHARD POTTS

*Human Origins Program, National Museum of Natural History,
Smithsonian Institution, Washington, DC 20560-0112*

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ABSTRACT The study of human evolution has long sought to explain major adaptations and trends that led to the origin of *Homo sapiens*. Environmental scenarios have played a pivotal role in this endeavor. They represent statements or, more commonly, assumptions concerning the adaptive context in which key hominin traits emerged. In many cases, however, these scenarios are based on very little if any data about the past settings in which early hominins lived. Several environmental hypotheses of human evolution are presented in this paper. Explicit test expectations are laid out, and a preliminary assessment of the hypotheses is made by examining the environmental records of Olduvai, Turkana, Olorgesailie, Zhoukoudian, Combe Grenal, and other hominin localities. Habitat-specific hypotheses have prevailed in almost all previous accounts of human adaptive history. The rise of African dry savanna is often cited as the critical event behind the development of terrestrial bipedality, stone toolmaking, and encephalized brains, among other traits. This savanna hypothesis has been countered recently by the woodland/forest hypothesis, which claims that Pliocene hominins had evolved in and were primarily attracted to closed habitats. The ideas that human evolution was fostered by cold habitats in higher latitudes or by seasonal variations in tropical and temperate zones also have their proponents. An alternative view, the variability selection hypothesis, states that large disparities in environmental conditions were responsible for important episodes of adaptive evolution. The resulting adaptations enhanced behavioral versatility and ultimately ecological diversity in the human lineage. Global environmental records for the late Cenozoic and specific records at hominin sites show the following: 1) early human habitats were subject to large-scale remodeling over time; 2) the evidence for environmental instability does not support habitat-specific explanations of key adaptive changes; 3) the range of environmental change over time was more extensive and the tempo far more prolonged than allowed by the seasonality hypothesis; and 4) the variability selection hypothesis is strongly supported by the persistence of hominins through long sequences of environmental remodeling and the origin of important adaptations in periods of wide habitat diversity. Early bipedality, stone transport, diversification of artifact contexts, encephalization, and enhanced cognitive and social functioning all may reflect adaptations to environmental novelty and highly varying selective contexts. *Yrbk Phys Anthropol* 41:93-136, 1998. © 1998 Wiley-Liss, Inc.

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Regarding the study of human evolution, it may be remarked that everybody talks about the environment, but nobody does much about it. The environment of human evolution has been a source of speculation since Darwin. Analyses of animal bones, pollen, and sediments have rendered a general portrait of Pliocene and Pleistocene habitats. Yet field projects are rarely designed specifically to recover high-resolution data on the ecological settings inhabited by early humans. Thus, there is a paucity of fine-scale spatial and temporal data that

can be linked to in situ evidence of hominins.¹ Usually, finding fossils and dating them have overshadowed any effort to deter-

¹Although it will take getting used to, the term *hominin* is now preferred in place of *hominid* to indicate the group of bipedal apes to which humans belong (genera *Homo*, *Australopithecus*, *Paranthropus*, and *Ardipithecus*) (Begun, 1992; Andrews, 1992; Andrews et al., 1996; Delson and Tattersall, 1997). The systematics of apes, including humans, now recognizes the growing body of evidence that humans and chimpanzees are sister taxa. Within the superfamily Hominoidea (apes) is the family of great apes (Hominidae). The hominid family includes the subfamily of African apes (Homininae), or hominines. The tribe rank of Hominini, then, is reserved for humans and related bipeds since the split from the chimpanzee lineage. Because early Pliocene bipeds no longer comprise a valid subfamily, I use the informal term *australopiths* to refer to them.

mine habitat contexts. A related problem is that most projects still focus on surface collecting, with unavoidably poorer taphonomic and contextual control than obtainable by digging. It is, however, only with exact stratigraphic relating of environmental data, fossils, and artifacts that answers may emerge about the range of habitats associated with particular species, when key expansions of habitat use occurred, or other substantive questions related to hominin adaptive change.

As fossil discoveries have sparked more than a century of ideas on the phylogenetic history of hominins, so research on the contexts of fossils and artifacts may come to stimulate a long phase of careful work on the ecological history of hominins. The immediate goal is to make this endeavor as systematic, empirically based, and comparative as possible. Clear definition of hypotheses and their test implications can help serve this goal.

The first purpose of this paper is to define pivotal hypotheses about the context of early human evolution and to lay out their test implications. Second, I will present some of the best-known environmental sequences from hominin sites as a preliminary series of tests. Environmental hypotheses can be divided into two types: those concerning adaptation and others concerning species turnover. Although the latter will be discussed briefly, our focus is on environmental hypotheses as they relate to adaptive evolution. This topic is of marked interest because adaptive explanations relate directly to the processes of natural selection and therefore help to discern how important evolutionary transformations took place.

Historically, the search for a convincing narrative of human evolution has stimulated strong interest—and guesswork—about the adaptive history of hominins. Thus, essentially every account of hominin evolution describes or assumes something about the milieu of human ancestors and the environmental problems that uniquely human features supposedly solved or overcame. Our focus here on environmental hypotheses with an adaptive flavor requires a framework for analyzing adaptation. So a third goal of this paper is to outline such a framework, which will show how paleoenvironmental studies

may contribute decisive data to the study of hominin evolution.

A final aim is to offer a brief primer to help anthropologists comprehend the barrage of paleoenvironmental methods, data, and interpretations published almost weekly in journals such as *Nature*, *Science*, *Quaternary Research*, and other scientific periodicals. A basic familiarity with isotope data, deep-sea cores, pollen analysis, loess climate curves, orbital parameters, and the main sources of paleoenvironmental evidence and habitat change is essential for understanding the contexts in which hominins evolved. To the extent that context is important—and Darwinian and later evolutionary biology established its fundamental role in organismal evolution—the field of paleoanthropology is, in this view, on the brink of novel ideas and data sets concerning the *how* and *why* of hominin evolution. Tremendous advances in the environmental sciences are forcing these developments to occur.

A PALEOENVIRONMENTAL PRIMER

An intricate system of heat and moisture circulation determines Earth's climate and has strong influence over the distribution of environmental zones and gradients. This enormous heating and plumbing system links the atmosphere, oceans, and land. It is affected by orbital cycles that determine the planet's variable dose of solar radiation. Volcanic activity and uplift of the crust also impact it. The basic processes and factors that therefore contribute to this circulation system are

- the amount and yearly pattern of solar radiation, determined largely by the planet's distance, orbital shape, and axial tilt relative to the sun;
- the amount of solar radiation absorbed and reflected by the atmosphere and by the ground surface;
- atmospheric processes, including evaporation, cloud formation, and rainfall;
- ocean and wind currents, two related patterns of circulation that redistribute heat and moisture in a biased manner around the globe;
- the size and distribution of ice caps, land masses, and major bodies of water, all of

- which create complex feedback with atmospheric processes;
- land uplift, which may interrupt or deflect ocean and atmospheric circulation currents and may create rain shadows that bias the distribution of rainfall near highlands; and
- volcanism, which alters climate by the eruption of airborne particles, and regional landscapes by the deposition of lava or tephra (e.g., ash, pumice).

A series of methods has been developed to measure the interactions and effects of these processes on Earth's environments. All of these methods are applicable to the period of human evolution; indeed, some of their most fruitful applications have been in the context of paleoanthropological research.

Marine oxygen isotope analysis

Interaction between the ocean and atmosphere lies at the heart of oxygen stable isotope analysis, a technique that has revolutionized paleoclimate studies since the 1950s. During evaporation, the stable isotope ^{18}O is enriched in ocean water as the lighter ^{16}O is preferentially released into the atmosphere.² In building their carbonate skeletons, certain marine microorganisms, such as foraminifera, absorb oxygen isotopes in proportion to the surrounding seawater. An ^{18}O -enriched ocean will thus result in a higher ratio of ^{18}O to ^{16}O in the microscopic shells. This transfer from ocean to foraminifera is also affected, though, by temperature. For every 1°C drop in water temperature, the proportion of ^{18}O to ^{16}O within the foramin shells is increased by about 0.22 parts per mil (‰). Thus the oxygen isotope ratio— $\delta^{18}\text{O}$ (delta 18-O)—in foraminifera is a measure, or proxy, of both temperature and evaporation.³

During glacial periods, oxygen (biased toward ^{16}O) that has evaporated from the sea becomes locked up in ice sheets as precipitation falls on land. Thus, foramin $\delta^{18}\text{O}$ fur-

nishes a record of glacial ice volume (which contains the sequestered ^{16}O) and temperature.⁴ Planktonic species of forams give information about sea-surface conditions, while benthic forams provide data about the deep-ocean environment, which is considered to reflect a wider record of ice (evaporation) and temperature history. This history is reconstructed by measuring $\delta^{18}\text{O}$ in foramin skeletons found in cores drilled from the deep sea. $\delta^{18}\text{O}$ curves are often thought to provide a measure of global climate, but this idea only refers to ocean temperature and ice volume, a history that may be decoupled from environments on land (e.g., deMenocal et al., 1993).

Figure 1 depicts the average curve for benthic forams from 70 Ma to the present. According to this curve, substantial global cooling of oceans took place during this period, with especially marked ice-sheet formation over the past 3 myr or so. By looking at specific ocean cores, however, one sees that this average cooling/drying trend is actually composed of many oscillations, the amplitude of which has risen over the past 6 myr (Fig. 2A). Sets of oscillations occurred within warmer and colder periods, forming a sequence of oxygen isotope stages (odd-numbered stages represent warm times; even refer to cold). Isotope stages 1–100 cover the past 2.5 myr. As depicted in Figure 2A, oscillation was particularly extreme over the past 700 ka. In this period, single excursions of the $\delta^{18}\text{O}$ curve (about 100 kyr long) encompassed 1.5‰ or more, which exceeded the total average change since the late Miocene (~1.4‰). Foramin records back to the late Oligocene (see Fig. 2B) indicate that the total range of $\delta^{18}\text{O}$ variation within 1 myr spans was fairly stable up through the Miocene. The total variation in each span consistently ranged between 0.3 and 0.8‰ up until 5–6 million years ago. At that time, the amount of variation increased significantly and continued to rise to the present (Potts, in press a). As we will see, different hypotheses about hominin evolution are sup-

²This process leading to isotope enrichment is called fractionation, in which the ratio of stable isotopes is altered during the transfer of an element (in this case, oxygen) from one medium to another.

³ $\delta^{18}\text{O}$ measurements reflect the relative concentration of the two isotopes and are expressed as ‰ variation from a standard isotopic reference, measured on a belemnite from the Pee Dee Formation (Cretaceous age), South Carolina.

⁴For periods in Earth's history when ice sheets were not present, the isotope ratio is primarily a measure of temperature.

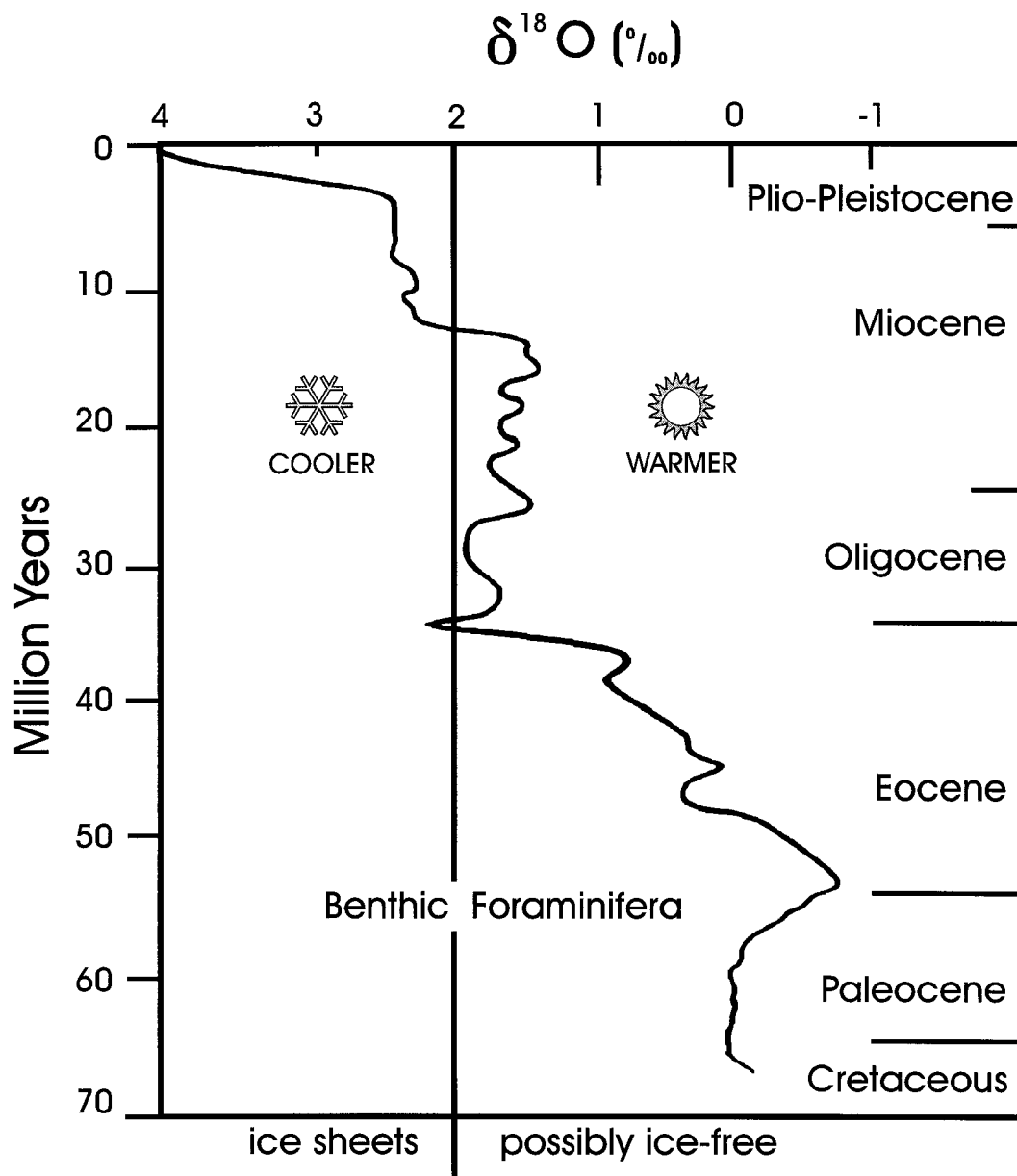
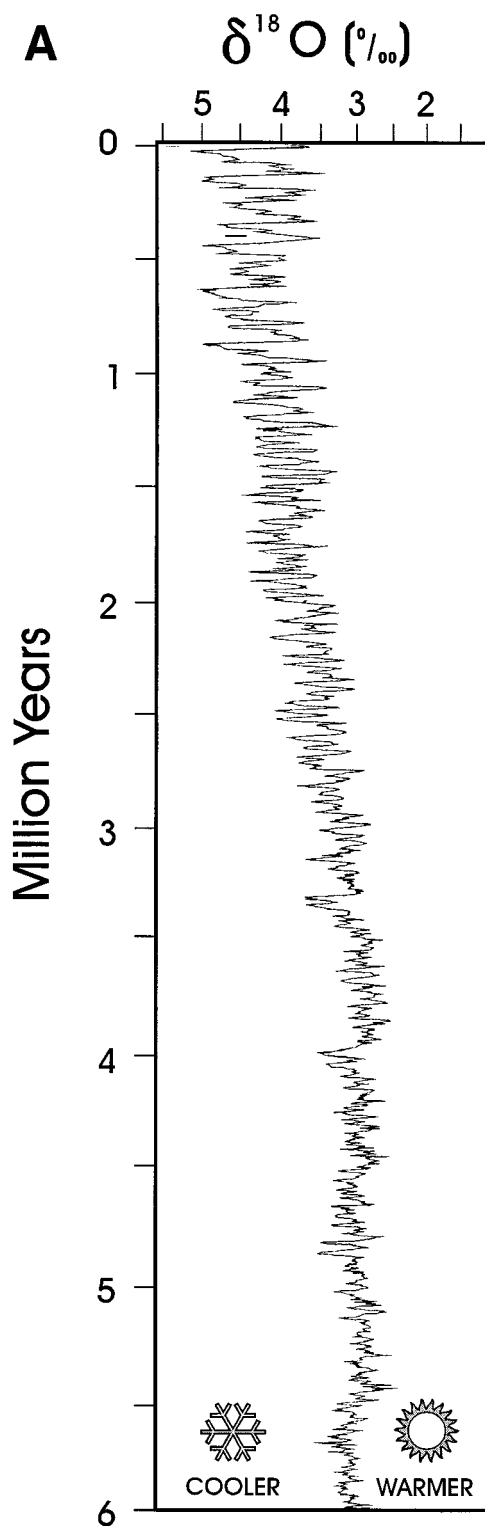


Fig. 1. Oxygen isotope curve (average) based on composite data from benthic foraminifera, 70 Ma to present (Miller et al., 1987).

ported depending on whether one focuses on the overall cooling trend (Fig. 1) or the oscillation (Fig. 2).

Study of the frequency and strength of oscillation, using a technique called spectral analysis, shows that $\delta^{18}\text{O}$ fluctuation occurs at certain periodicities. For the past 1 mil-

lion years, the dominant cycles are approximately 100 kyr and 41 kyr long and a dual cycle of 23 kyr and 19 kyr. These cyclicities match variations in Earth's orbit around the sun, an idea proposed by Croll (1875) and then expanded by the mathematician Milankovitch (1941). A complete eccentricity



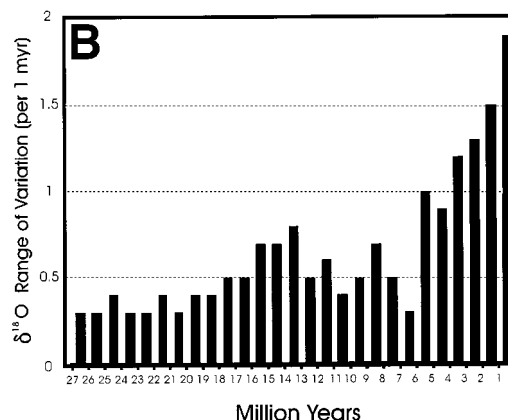
cycle (the circular-to-elongate shifting of Earth's elliptical orbit around the sun) takes approximately 100 kyr. Obliquity (the changing tilt of the planet's axis of rotation relative to the sun) varies between about 21.4° and 24.4° on a cycle 41 kyr long. Precession of the equinoxes, due to Earth's axial wobble, changes the timing of the seasons relative to the distance from the sun on a cycle lasting about 21 kyr. Over this cycle, the northern hemisphere is tilted toward the sun at successively different points in Earth's orbit.

These cycles affect the total amount of incoming solar energy (insolation), and they interact to create complex fluctuation in insolation, which is remarkably registered in the shells of forams and the oxygen-isotope curve. It is assumed, therefore, that these orbital variations have a prevailing influence over global climate, including overall cooling during the late Cenozoic and the rate and range of oscillation. An important milestone of Cenozoic climate change was the onset of high-latitude glaciations starting around 2.8 Ma, an event that has been linked to events in hominin evolution.

Ocean dust records

Dust plumes arising from continents result from strong seasonality of rainfall and

Fig. 2. **A:** Oxygen isotope curve 6 Ma to present, based on benthic foraminifera (Shackleton, 1995). **B:** Range of variation in oxygen isotope values in 1 million year intervals from late Oligocene (27 Ma) to present. Based on data from Miller et al. (1996), Wright and Miller (1992), Woodruff et al. (1981), Shackleton (1995), and Prentice and Denton (1988). (Reproduced from Potts, in press a, with permission of the publisher).



in the winds that carry the dust to the ocean. Aeolian dust accumulations found in ocean sediment cores thus provide a record of long-term change in seasonality and prevailing wind patterns. These records may reflect the history of continental vegetation cover, since large areas of open vegetation and desert enhance the chances of erosion and wind transport of land detritus.

In a detailed study of cores off the west and east coasts of Africa, deMenocal (1995; deMenocal and Bloemendal, 1995) has shown that African climate (and vegetation cover) was highly variable from early Pliocene to the present (Fig. 3). Spectral analysis (right side of Fig. 3) indicates a change in oscillation at around 2.8 Ma, from a dominant frequency of 23 to 19 kyr (precession) to one of 41 kyr (obliquity). Other shifts occur at 1.7 and 1.0 Ma, at which point the 100 kyr frequency begins to dominate. These findings suggest that African climate variation was tuned to orbit-related changes in insolation. These shifts represent periods of markedly increased aridity at 2.8, 1.7, and 1.0 Ma; the origin of certain hominin species in Africa after 2.8 Ma, therefore, may reflect the rise of an arid-adapted biota (deMenocal, 1995). However, as noted by deMenocal and Bloemendal (1995), these dates primarily signal substantial rises in the overall variance, or amplitude of fluctuation, rather than a permanent shift toward a drier, more open environment (Fig. 3).

Ice cores

Accumulation of ice in glaciers, ice sheets, and ice shelves results from precipitation of water evaporated largely from the ocean. Thus, $\delta^{18}\text{O}$ analysis of cores drilled from major ice bodies yields a high-resolution record of climate, which is the inverse of deep-sea $\delta^{18}\text{O}$. Particularly informative records into the middle Pleistocene have been obtained from Greenland and Antarctica. One significant finding from the Greenland cores is evidence of extremely rapid oscillations during certain time intervals. Known as Dansgaard-Oeschger events, these oscillations last around 1,000 years; during these events, fluctuations between interglacial warmth and severe cold take place over a century or even a decade in some cases

(Broecker and Denton, 1990; Taylor et al., 1993; Dansgaard et al., 1993). Based on these findings, it has been argued (e.g., Calvin, 1996) that hominin adaptability evolved in response to large, short-term fluctuations in middle or high latitudes.

Evidence of such abrupt variation, however, is absent in the Antarctic ice cores (Jouzel et al., 1993), suggesting that the oscillation events may be largely a northern hemisphere phenomenon. A partial explanation is that rapid cooling may correspond with periods of iceberg discharges (or rafting) into the North Atlantic (known as Heinrich events); by adding fresh water to the sea, these discharges may suddenly reduce the heat-conveying effect of one of the most important ocean circulation systems, the North Atlantic Deep Water, thereby causing abrupt cooling of 5–8°C (Bond et al., 1992; Stauffer et al., 1998). Deep-sea data from the North Atlantic show that such abrupt cooling-warming cycles occurred regularly back to at least 1 Ma (Raymo et al., 1998).

Sedimentary environment

Basic geologic analysis at hominin sites includes field recording and mapping of sediments, describing major depositional environments (lithofacies), and logging stratigraphic change. Certain types of deposits, such as caliches, and the presence of particular minerals are indicative of specific environmental conditions (e.g., aridity, rainfall). Other deposits, such as widely distributed tephra, permit ready correlation between distant locations. Correlation of stratigraphic sections over several kilometers enables the reconstruction of paleogeographic settings on a basinwide scale. Such reconstructions have proved powerful in interpreting the adaptive contexts of hominins at Olduvai, Turkana, and other localities (Hay, 1976a; Brown and Feibel, 1991).

Lake sediments

Lakes may provide habitats for diatoms or other environmentally sensitive organisms (e.g., ostracods). Analysis of these organisms can yield a precise history of lake depth, salinity, and alkalinity—factors that are strongly influenced by climatic and tectonic variations. Study of diatom species in the

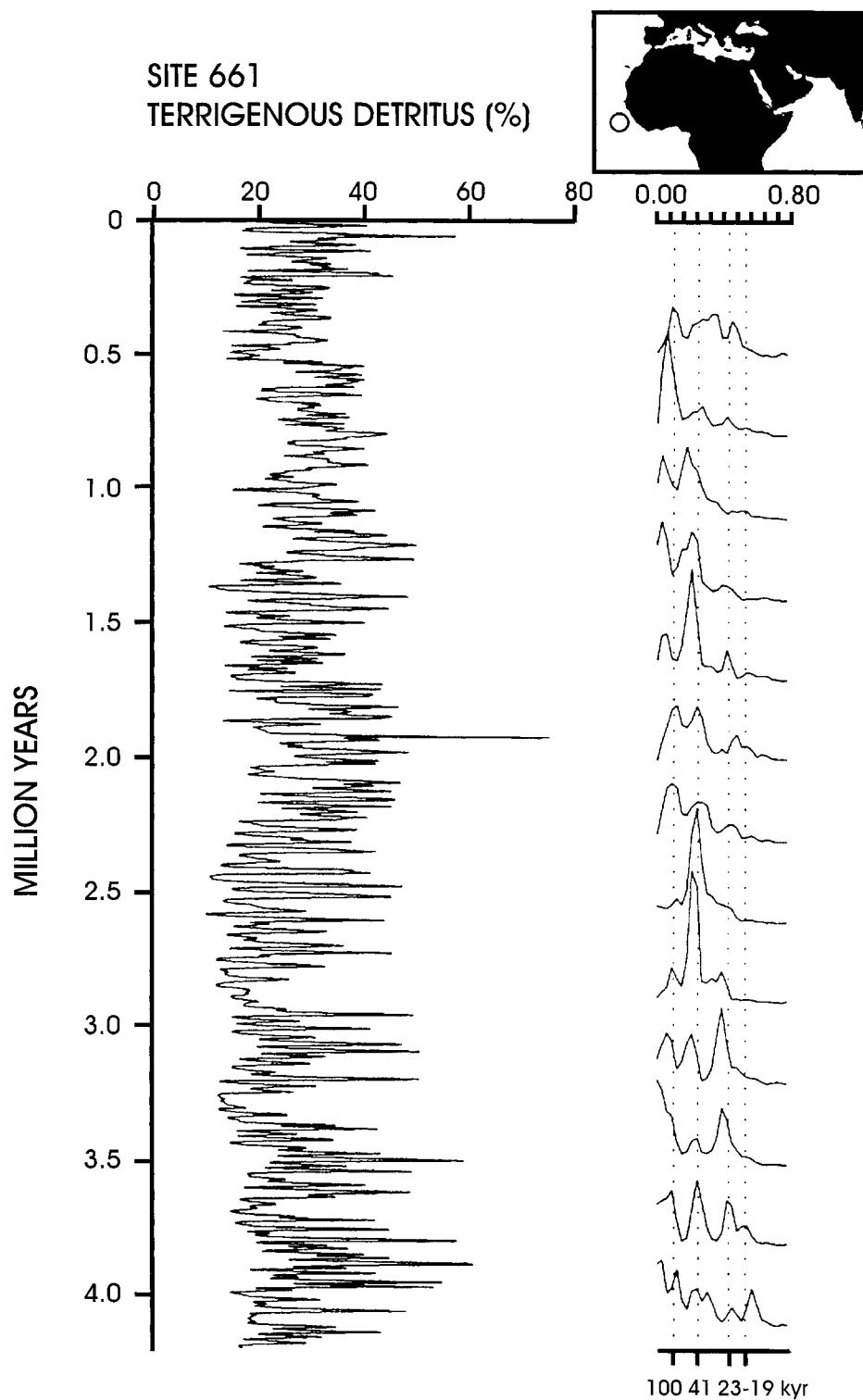


Fig. 3. Continental dust (%) measured in the ocean core from Site 661, off the west coast of Africa, 4 Ma to present. Percentage aeolian dust was calculated using magnetic susceptibility, a measure of the concentration of magnetic particles typically found in wind-blown dust. The power spectrum (right) is an analysis of variance in the oscillation time series. This drilling site is one of seven on which deMenocal's analysis is based (deMenocal and Bloemendal, 1995; deMenocal, 1995).

Olorgesailie Formation, for example, has helped to establish the history of an ancient lake basin inhabited by hominins (Owen and Renaut, 1981; Potts, 1994) and to calibrate rates of environmental change faced by the toolmakers (see below).

Loess sequences

Thick sequences of alternating loess (wind-blown sand) and soil (paleosols) occur throughout vast regions of Asia and Europe. Loess layers represent times when vegetation cover was sufficiently low to allow buildup of aeolian material. The soils, on the other hand, are often organic-rich due to thick vegetation cover at the time of soil formation. Loess sequences of north-central China have been especially well studied and provide a detailed record of environmental change. Over the past 2.5 myr, at least 44 major shifts from cold to warm conditions have been documented.

Environmental interpretations are based on the degree of loess and soil weathering, fossil pollen and fauna, carbonate content, and magnetic susceptibility. The latter method measures the concentration of magnetic grains, which is especially high in fine dust blown from distant sources. This fine component dominates during warm, wet periods, while relatively coarse grains from local sources tend to be deposited during cold, dry eras. Thus, high susceptibility measurements are found in the soils and low ones in the loess layers. These measurements offer a record of oscillation in climate and vegetation. Figure 4 illustrates a section of the Luochuan loess sequence, in which strong fluctuations between cold, open steppe and warmer, wooded to forested conditions have been documented (Liu, 1988; Kukla and An, 1989). Because they cover huge continental areas, loess-soil deposits offer a potentially powerful method of determining environmental sequences in temperate latitudes occupied by early hominins.

Fossil pollen sequences

Pollen is deposited as "pollen rain," samples of which can be characterized by the percentages of different vegetation components, known as a pollen spectrum. The basic components are usually arboreal (trees

and shrubs) and nonarboreal (herbs) pollen (abbreviated AP and NAP, respectively). Percentage AP reflects the density of tree cover, though this provides only a rough measure in low latitudes since tropical trees have lower pollen production than grasses and other NAP. Divisions of NAP often include grasses (Gramineae), aquatics (such as *Typha* and Cyperaceae), and the C/A group (Chenopodiaceae/Amaranthaceae). The first indicates the relative density of grass cover, especially when aquatic taxa are factored out. The last group can be a good indicator of aridity in African settings, since most of the C/A plants come from saline soils and dry streams. Environmental interpretation of pollen spectra is based on modern analogues and thus requires careful comparison of past and present samples and preservation conditions. The lack of accurate analogues for past climates, particularly glacial conditions, can sometimes be offset by incorporating other evidence (e.g., in Europe, the representation of fossil beetles, which are climatically sensitive). The sum of certain AP taxa is often used as a climate index, although the validity of this approach has been questioned. In East Africa, fossil pollen analysis has yielded a sequence of general vegetation and climate reconstructions for localities such as Olduvai, Turkana, and Hadar; while in Europe the coring of peat bogs has enabled high-resolution analysis of precipitation and temperature based on pollen (Bonnefille, 1995; Guiot et al., 1989, 1993; Woillard, 1978). Figure 5 illustrates a detailed series of climatic fluctuations indicated by pollen spectra from the sediment core at Les Echets, France.

Stable isotope analysis of soils

Under certain conditions, buried soils, or paleosols, preserve organic residues and carbonate deposits that bear a stable-isotopic signal of past vegetation. Interpretation of vegetation is based on the photosynthetic chemistry of plants and the signature it leaves in soils. Most plant species undergo one of two distinct photosynthetic pathways; one involves three carbon atoms and the other four (thus C₃ and C₄ plants). C₄ plants are virtually all grasses adapted to hot, dry conditions and low CO₂ concentrations in

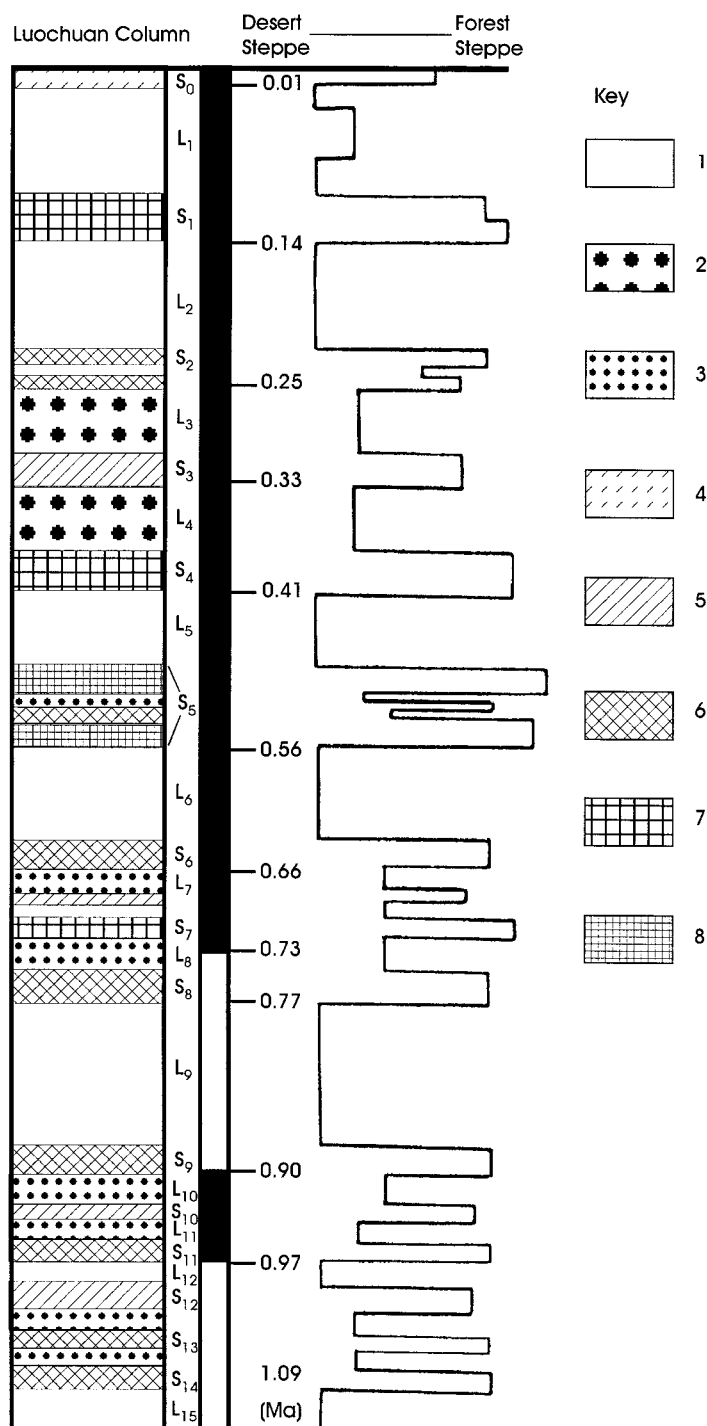


Fig. 4. Sequence of loess layers (L_n) and paleosols (S_n) from Luochuan, north-central China, 1.1 Ma to present, and environmental interpretation based on the degree of loess/soil weathering, magnetic susceptibility, pollen, and carbonate analysis. 1–3, weakly, moderately, and strongly weathered loess, respectively; 4, black loam; 5, carbonate cinnamon soil; 6, cinnamon soil; 7, leached cinnamon soil; 8, dark cinnamon soil (Liu, 1988).

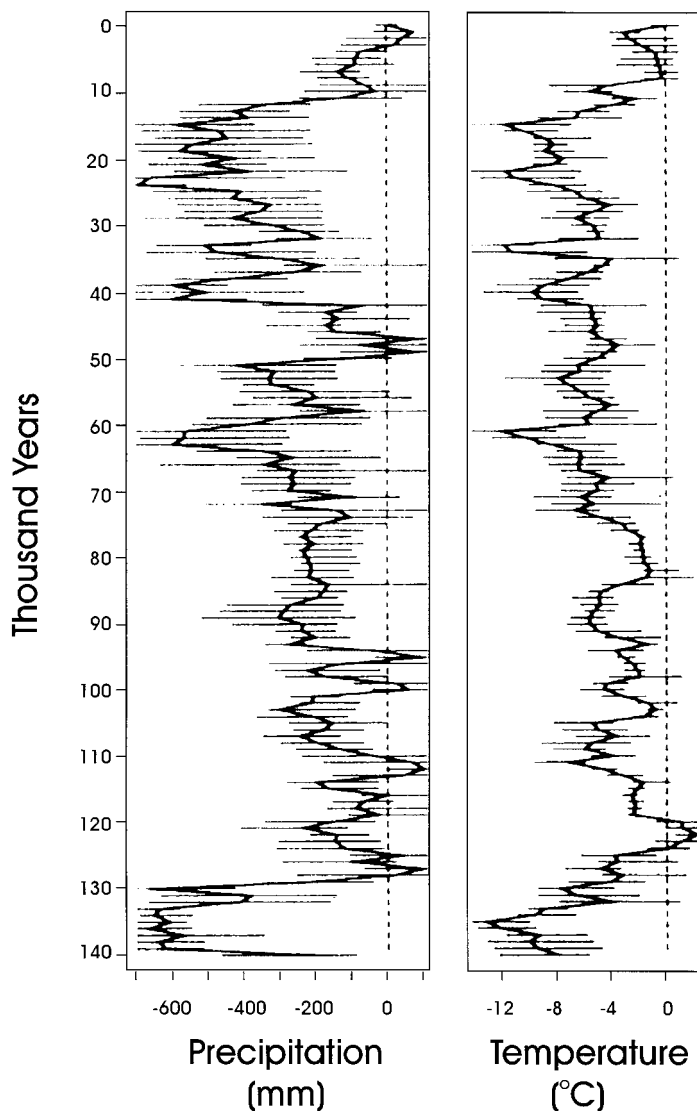


Fig. 5. Estimates of mean annual precipitation and temperature, expressed as deviations from present values (800 mm and 11°C) plus confidence intervals, 140 ka to present, based on pollen recovered from the Les Echets pollen core, eastern France (Guiot et al., 1989).

the atmosphere. C_3 plants include woody species, herbs, and grasses adapted to cool growing seasons and shade. The two categories have nonoverlapping distributions of $\delta^{13}O$ (ratio of carbon isotopes $^{13}C/^{12}C$). In temperate zone soils, therefore, ^{13}C can indicate change in climate or atmospheric CO_2 . In tropical lowlands, this measure may also indicate vegetation structure along the gradient from heavily wooded to open grassland habitat. In addition, the oxygen isotope ratio can be measured in soil carbonate and is correlated with mean annual temperature.

Combined analysis of $\delta^{13}C$ and $\delta^{18}O$ of ancient soils, therefore, can allow quite specific interpretation of the complex relationship between soil and atmospheric chemistry, vegetation, and temperature (e.g., Cerling and Hay, 1986; Cerling, 1992; Cerling et al., 1997; Ambrose and Sikes, 1991). Isotopic study of widely exposed paleosols has also enabled detailed comparison to modern landscape analogues, which may be extended to reconstruct the mosaic of wooded, grassy, and wetland habitats in strata bearing early human artifacts (Sikes, 1994; Sikes et al., in press).

Faunal analysis

Relative abundance of different animal species permits a general characterization of habitat, assuming that certain taxonomic groups correlate with specific habitats in both the past and present (e.g., Vrba, 1975; Potts, 1988; Shipman and Harris, 1988). A different array of methods uses functional morphology to test for definitive anatomical indications of environment. This approach allows an ecomorphic (as opposed to a taxonomic) characterization of the biota and associated habitats without assuming particular taxon-habitat correlations. Methods of ecomorphic analysis have increasingly been applied to the faunas of early hominin sites (e.g., Andrews, 1989; Plummer and Bishop, 1994; Kappelman et al., 1997; Reed, 1997).

Summary

Development of these and other methods of environmental interpretation has progressed impressively over the past several decades. The contexts in which these methods can be applied include deep-sea cores, peat bogs, soils, and many diverse types of sediment. The methods can in many cases go beyond a general history of climate and habitat to offer a quite detailed picture of the adaptive contexts faced by early hominins.

A FRAMEWORK FOR ANALYZING ADAPTATION

The process of adaptation, natural selection, involves the relationship between an organism and its surroundings. An organism's environment (at least aspects that affect survival and reproduction) influences the traits that persist, increase, and spread through a population. Traits positively affected by the process of biased reproduction are called adaptations. The analysis of adaptations thus may afford insights into both the process of natural selection and the environmental context in which evolution has occurred. The purpose of this section is to define an analytical framework that shows how paleoenvironmental data from hominin sites may contribute to the study of adaptive evolution in early humans.

The field of biology is divided between two main approaches to the concept of adapta-

tion (Amundson, 1996; Endler, 1986). The first is a nonhistorical approach, which defines an adaptation solely in terms of the current, observed benefits that a particular trait offers to an organism (Bock, 1980). The process of origin (natural selection) and thus the history of a given trait are, by this definition, less relevant to deciding whether a trait is an adaptation. A nonhistorical definition of adaptation, then, concerns simply the contribution of a trait to current fitness (Fisher, 1985).

The second is a historical approach, which focuses not only on fitness but also on the process by which adaptation occurred. Accordingly, an adaptation is a trait generated by natural selection due to its fitness benefits. This approach focuses, then, on the history of a trait. It allows the possibility of studying and citing the selective causes that underlie a particular adaptation. With hominin evolution, we are very much interested in history. Thus, the second approach is adopted here. For one thing, current benefit (the basis for defining an adaptation in the nonhistorical approach) has no meaning when looking at characters of extinct hominins. In an evolutionary perspective, moreover, current benefit even in living humans does not always give a true picture of a trait's original advantage or the conditions under which it evolved. In a historical analysis, then, adaptation is the result of natural selection, and the analysis of adaptation entails an assessment of how the prevalence of a trait in the fossil record may have resulted from this process.

But how does one recognize natural selection, or at least its results, in the fossil record? The first order of business is to define a trait, feature, phenotype, or character (all considered synonyms here) or even a complex of traits or a definable morphological or behavioral pattern. The definition of a feature or overall phenotype provides the basis for examining function, benefit, and evolutionary setting.

In a historical approach, an analysis of adaptation must also be based on the process of natural selection itself. As summarized by Lewontin (1970), the process has three necessary and sufficient conditions: variation, heritability, and differential fit-

ness. For selection to operate, the units of evolutionary change (e.g., specific phenotypic features) must vary. The variations must be inherited (e.g., the phenotypes must relate to specific genetic variations). And the variations must differ in their representation in later generations.

These three conditions furnish an initial framework, but many other factors enter into an analysis of adaptation. Differential fitness occurs presumably due to certain benefits that one variant offers compared to others (alternative phenotypes). So it is essential to determine what those benefits were (or are), especially how a trait's structural design or pattern of expression provided a selective advantage. Each beneficial feature may also have its share of costs, which cannot outweigh the benefits if a feature is to increase via natural selection. The adaptive evolution of a feature is often assumed to take place in a competitive setting, and its increase may have serious repercussions for other individuals within that setting, which could affect the increase and spread of the feature.

Furthermore, benefits, costs, and competition all take place in relation to particular environments. This is one reason the analysis of adaptive evolution involves environmental reconstruction. The stability or dynamics of environmental change may also have an impact on natural selection. The different time scales of environmental fluctuation may affect natural selection and, as we will see, may determine the kind of traits that are ultimately represented in a population.

Finally, a growing number of evolutionary biologists believe that lineages themselves possess adaptations, referring to characteristics (e.g., geographic range, habitat variety, dietary versatility) that go beyond the makeup of an individual organism (Vrba, 1989; Jablonski, 1987). Since these characteristics may impact the survival of populations over time, they may also affect the success of particular features originated by conventional, individual-level natural selection.

A basic framework for the analysis of adaptation, then, can be conveyed by a series of questions (Table 1) that take into

TABLE 1. A 13 part framework for the analysis of adaptation

1. How is a particular feature (morphological structure, behavior, phenotypic system or complex) manifested? What is its structure, or what are its characteristics?
2. What is the function of a particular feature? What is it designed to do? What selective advantages does the feature offer to an organism?
3. What "currencies" of advantage or success does the feature provide to the organism? An advantage in survivorship? A direct reproductive advantage? Does the feature raise the organism's efficiency or economy (Steudel, 1994)? Ultimately, how does the feature contribute to the genetic fitness of the individual?
4. Besides its beneficial function, does the feature have any costs to the organism? What are those costs?
5. What is known about the feature's heritability?
6. What is known about the feature's development (growth and expression during the life cycle)? What are the necessary environmental parameters for proper development?
7. Does the feature (e.g., a particular behavior) have any repercussions (costs or benefits) for other organisms? In other words, what was the competitive and/or social context in which the feature evolved or currently functions?
8. In the context of natural selection, when did the feature originate? In what environmental context or conditions did it evolve? What advantages did the feature offer within that original context? Did the feature represent a response to a specific environment or to diverse surroundings? Do the original advantages and environmental context still apply to the organism that possesses the feature?
9. What were the options or alternative phenotypes (e.g., the ancestral condition) available to the organism when the specific feature evolved?
10. Historically, is the feature a by-product of adaptive change in another trait (in which case it is not an adaptation), or did the feature evolve due to specific benefits of a task it performs or contributes to?
11. Does the feature serve its original function, or is it an exaptation (co-opted for some other function [Gould and Vrba, 1982])?
12. Over what time scale does the feature assist the organism? Daily? Seasonally? Does it offer resilience to environmental variations faced over a lifetime? Does it offer flexibility to a population over longer periods of environmental change?
13. Are there lineage-level adaptations—that is, features of a lineage (rather than of an individual) that enhance its ability to spread, persist, or diversify when compared with other, related lineages? If natural selection can take place at the species level, what kinds of features might be involved in this process?

account phenotype definition, the operation of natural selection, and the factors that affect differential fitness.

The analysis of adaptation is tricky largely because the questions posed in Table 1 are difficult to answer and any answers put forth are usually controversial. As debate

about the evolution of the human chin demonstrates (Gould, 1977), even the first step—defining a trait subject to natural selection (Table 1, questions 1–3)—can create controversy, partly because traits can emerge as a by-product of adaptive modification (question 10). Besides these correlated effects, developmental (e.g., embryological) constraints are ubiquitous, which place boundaries on trait variation, the raw material acted on by natural selection, and thus on adaptation itself. Structural design, the benefits, and the costs of morphological traits can be considered with some success by functional anatomists. But specialists interested in past behavior (e.g., australopith bipedality, late Pliocene stone flaking) usually have greater difficulty evaluating design properties, frequency of occurrence, heritability, and the advantage over alternative behaviors. In fact, very little is known about the heritability of even simple structures and behaviors unique to humans. The heritability of characters (e.g., megadontia) that distinguish extinct hominins, moreover, is largely inaccessible except perhaps by analogy to living mammals that possess similar traits.

Given these difficulties, the study of early hominin adaptation is largely left with the analysis of context (Table 1, question 8). The questions of time, place, and environmental setting are essential to all evolutionary analyses of adaptation. The selective history of a trait is reflected in part by when, where, and the conditions or surroundings under which that trait first became apparent in the fossil record and began to characterize a particular lineage or clade. The precise definition of hypotheses relating past environments to the emergence of unique hominin traits, therefore, helps to galvanize research on early human evolution.

ENVIRONMENTAL HYPOTHESES OF HOMININ EVOLUTION

A concise history

Challenges of the savanna. Over much of the twentieth century, scientists thought that human evolution entailed a simple trajectory from apelike to humanlike and that this process was promoted by the challenges of an open savanna. In his book *The Evolu-*

tion of Man, Elliot Smith (1924:40) described the terrestrial domain of early human ancestors as “the unknown world beyond the trees”—a place of novel food sources, quite distinct from the “land of plenty” of the apes. Dart (1925) took this idea to dramatic heights. To convey the selection pressures that drove human evolution, Dart drew an analogy to the southern African veldt. The early australopiths, he argued, confronted many dangerous predators, a relative scarcity of water, and fierce competition for food, all of which he ultimately encapsulated in the killer-ape scenario (Dart, 1953). Later views, such as the dietary hypotheses of Robinson (1954, 1961a,b) and Jolly (1970), also explicitly related hominin origin to a shift from forested/wooded “apelike” habitat to an open savanna setting.

Intrinsic and extrinsic approaches. If indeed human evolution followed a progressive path from apelike to humanlike, it could also be reconstructed by extrapolating up from the anatomical, behavioral, and ecological characteristics of apes and other nonhuman primates and extrapolating down from ethnological data on human foragers. The paper “Ecology and the Prothominids” by Bartholomew and Birdsell (1953) made explicit this approach to modeling human evolution. This paper was the first to draw attention to key theoretical aspects of early human ecology, including population density and dynamics, territoriality, foraging, energetics, body size, and sociality. Yet no environment was reconstructed, and no ideas were offered about the interaction of early humans with specific environmental variables. Implicit in their discussion was that the environment of hominin evolution was already generally known. It involved, at first, increasingly arid, savanna conditions in Africa, followed by increasingly cool, glacial conditions in northern latitudes.

Despite their emphasis on ecology, Bartholomew and Birdsell (1953) provided an outline for an intrinsic account of hominin evolution whereby adaptive change resulted largely from responses within populations over time without regard to change in external conditions. All they required was the basic scene, a relatively open savanna. Their

argument followed Darwin's (1871) basic scenario: bipedality (ground living) and small canine teeth implied that the earliest hominins used tools, which permitted an expanded diet, including animal foods; thus, hunting in bands and changes in sociality occurred as one adaptive change led to others. Washburn (1960) refined this type of explanation, and placed tools at the center of an evolving system in which each novel adaptation fostered others in an intricate series of feedback loops. "Tools, hunting, fire, complex social life, speech, the human way and the brain evolved together to produce ancient man of the genus *Homo*" (Washburn, 1960:63). Again, Washburn's intrinsic feedback model was not without context. If bipedal tool use initiated the cause-and-effect process of hominin evolution, life in the open plains provided the crucial, initial setting (Washburn, 1960).

Washburn's influence and interest in intrinsic accounts (as opposed to extrinsic accounts, which interpret evolutionary events in relation to environmental change) may explain why many paleoanthropologists in the 1950s to 1970s paid little attention to environmental context. In two classic volumes on hominin evolution (Washburn, 1961, 1963), none of the 35 papers focused primarily on environmental settings, and only seven considered the subject.⁵ This approach was echoed in the influential four volume set *Perspectives on Human Evolution* published between 1968 and 1978 (Washburn and Jay, 1968; Washburn and Dolhinow, 1972; Isaac and McCown, 1976; Washburn and McCown, 1978). The only articles on paleoenvironmental context were in Volume 3 (six of its 21 chapters). Two dealt with Miocene faunas and floras (Van Couvering and Van Couvering, 1976; Andrews and Walker, 1976), two others considered environmental evidence from specific hominin-bearing basins (Olduvai, Omo) (Hay, 1976b; Howell, 1976), and two chapters highlighted the general context of the

East African rift (Isaac, 1976; Bishop, 1976). It is interesting to note that Bishop's paper demolished the "myth of a Pliocene drought" (p. 40) championed by Dart, which had fueled the view that early human evolution was a response to a sharp shift from moist forest to arid savanna. Moreover, the papers concerning Miocene sites showed that early apes lived in a complex mosaic of environments, including closed and relatively open vegetation. These papers were among the first to hint at the intricate environmental history related to ape and human evolution. Isaac (1976:133) ended his article by noting the paucity of contextual studies and compared the existing information base about East African paleoenvironments to an "exposed tip of an iceberg."

While most anthropologists took an intrinsic approach, geologists and vertebrate paleontologists showed strong interest in paleoenvironmental data and the reconstruction of early hominin settings. Thus, in Howell and Bourlière's (1963) volume *African Ecology and Human Evolution*, almost all of the 19 papers discussed the importance of contextual data (the main exception was that by DeVore and Washburn). The papers (e.g., by Butzer) included cautions about simplistic linkages between higher latitude glacial sequences and lower latitude environmental history. Other papers surmised that complex tectonic and climatic events were interwoven in creating the environmental history of Africa (e.g., papers by Bishop and by de Heinzelin). Several papers showed evidenced that Pleistocene Africa underwent a complex series of habitat changes between moist and dry and between forested and open (e.g., papers by Moreau, Monod, Grove and Pullan, and de Heinzelin). Articles by Biberson and by Howell and Clark were particularly successful in placing Pleistocene stone technologies and behavior in specific sedimentary, vegetational, and climatic contexts.

Later volumes by Bishop and Clark (1967), Butzer (1971), and Bishop (1978) continued to emphasize the importance of environmental (sedimentary, geomorphological, taphonomic, and ecological) settings for understanding hominin evolution. More than half of the articles published in Butzer and Isaac's

⁵Four papers (by Chance, Oakley, Hallowell, and Sauer in the 1961 volume) reiterated the general view that the earliest ancestors inhabited the African savanna while later hominins lived in an ice-age context. Three others (by Mayr, Dobzhansky, and Harrison and Weiner in the 1963 volume) discussed environments as a theoretically important determinant of natural selection, adaptive change, and speciation in hominins.

(1975) *After the Australopithecines* and nearly one-third of the contributions to Jolly's (1978) *Early Hominids of Africa* focused specifically on the climatic, geologic, and paleoecological contexts of hominin sites.

By the early 1980s, a wide range of environmental data was becoming available due to a surge in paleoclimate studies and detailed work by field geologists at fossil and archeological sites. Laporte and Zihlman (1983) made a strong case for the idea that environment was a major driving force in early human evolution. In their view, adaptive change in apes, including Pliocene hominins, represented responses to either new environments or physical access to existing environments (e.g., via land bridge). They argued that global cooling reduced tree cover over large regions, and African uplift and rifting created a rain shadow effect (drying) in the eastern part of the continent. These factors caused the spread of the savanna mosaic, marked by strongly seasonal rainfall, discontinuous distribution of trees, and heat-adapted, drought-resistant vegetation. Echoing earlier authors, Laporte and Zihlman (1983:106–107) posited that the “challenges of the savanna-mosaic” caused ground-dwelling in a prehominin ape and bipedality in the earliest hominins. Two-legged walking enabled mobility and carrying of food and water over long distances as resources became more widely (patchily) distributed. Finally, they noted that the “origin of hominids [sensu stricto] is not an isolated evolutionary event, but rather is part of the overall radiation of African hominoids; nor is it an unusual ecological occurrence. The hominids are only one of several mammalian groups that include the pigs and bovids that were able to exploit the savanna-mosaic habitat that had become widespread by the end of the Miocene” (Laporte and Zihlman, 1983:108).

Turnover hypotheses. At about the same time, Vrba (1980, 1985, 1988; also Brain, 1981) began to present an important idea, known as the turnover pulse hypothesis, which expanded these same themes—climatic forcing of evolution, a Pliocene aridity shift, and coincident change in hominins and other mammalian lineages. Turnover

pulse refers to a concentration of speciation and extinction events (i.e., turnover) in a brief period of time as a result of environmental change. According to Vrba's original hypothesis, many different African mammalian clades were involved in a turnover episode at 2.5 Ma. Synchronous change in multiple groups was caused by a shift from warm, moist conditions to a cooler, drier, and more open habitat. This environmental event was forced by global cooling, manifested as a sharp transition (^{18}O enrichment) in the deep-sea isotope record. The hypothesis thus posits a strong causal link between hominin evolution and global climatic events. Accordingly, the origins of *Homo* and of the robust australopiths at about 2.5 Ma were considered part of the turnover pulse. Since a speciation pulse in grazing bovids occurred at this same time (e.g., Vrba 1985, 1988), *Homo* and *Paranthropus* were also deemed part of the Pliocene arid, open-grassland biota of Africa. Vrba et al. (1989) posited two other turnover pulses, about 5 Ma and 0.9 Ma, which also appeared to coincide with periods of global cooling and continental drying. The origin of the Hominini, on the one hand and the extinction of robust australopiths, coupled with the dispersal of *H. erectus* into Eurasia, on the other were thought to be correlated with these environmental shifts.

The original hypothesis has been revamped in two main ways. Since the mid-1980s, paleoclimatologists have broadened the age estimate of Pliocene global environmental change. Based on the deep-sea oxygen isotope record (Fig. 2A), for example, a major shift in global ice sheets began as early as 2.8–3.0 Ma, with the most significant change between 2.8 and 2.4 Ma (e.g., Prentice and Denton, 1988). The deep-sea dust record (see Fig. 3) also indicates a major change in cyclicity beginning around 2.8 Ma. Thus, the pulse in the late Pliocene turnover pulse hypothesis has been broadened; the target interval has been extended from a point in time (2.5 Ma) to a span as wide as 400 kyr. According to this broader pulse model, key events in hominin evolution and concerted turnover in other mammals should be evident from 2.8 to 2.5 (or 2.4) Ma rather than randomly distributed

throughout the entire 3.5 myr span of the Pliocene (Prentice and Denton, 1988). In Vrba's (1995b) view, the turnover pulse in Africa began 2.8 Ma but became apparent in the fossil record only between 2.7 and 2.5 Ma. This is the first way in which the hypothesis has been altered.

The second way involved refining the test implications of the turnover pulse model and broadening its theoretical basis. Building on a synthetic view called habitat theory, Vrba (1992, 1995a) posits that the record of a turnover pulse should depend on the breadth of resources and habitats used by organisms. First and last appearances will be synchronized or spread out according to the ecological tolerances of different lineages. A global cooling event causing the spread of savanna between 2.8 to 2.5 Ma thus should have caused turnover in specialized organisms first and in more generalized organisms later. Furthermore, it should cause a larger number of first appearances in arid-adapted taxa (e.g., hominins and grazing bovids) and more last appearances in warm, woodland-adapted species.

Vrba has been assiduous in testing the turnover pulse idea. Many appearances and disappearances of bovid lineages in the African fossil record are clustered around 2.5 Ma (Vrba, 1985, 1988, 1992, 1995b). Grazing bovids (alcelaphines such as wildebeest, hartebeest, and topi and antilopines such as gazelles) contributed strongly to the first appearances. This supports the idea that aridity and grassland expansion were the environmental causes of bovid lineage turnover. Vrba (1985, 1988) has also emphasized Wesselman's (1984) conclusion (based on a study of micromammals from Omo, Ethiopia) that forest taxa prevalent at 3 Ma gave way to xeric-adapted, open vegetation taxa between 2.4 and 2.5 Ma. In the volume *Paleoclimate and Evolution, with Emphasis on Human Evolution* (Vrba et al., 1995), papers concerning paleoclimate and vegetation tend to confirm that large environmental change occurred between 2.8 and 2.5 Ma. Many of these papers, however, stress the evidence for strong fluctuation at this time rather than a simple cooling or aridity shift. Conclusions drawn from African bovids, micromammals, and hominins are said to sup-

port the turnover pulse idea (Vrba, 1995b; Wesselman, 1995), though an analysis of suids and hominins argues strongly against the hypothesis (White, 1995).

The pulse hypothesis has been questioned on other grounds, however, and countered by what may be called the prolonged turnover hypothesis (Behrensmeyer et al., 1997; McKee, 1996). Building on earlier observations (Feibel et al., 1991), a recent study by Behrensmeyer et al. (1997) focused on the Turkana-Omo basin since this area offers the richest and best calibrated record of African fossil mammals in the crucial span between 3 and 1.8 Ma. Taking sampling variation (rises and falls in fossil samples over time) into account, this study found no statistically significant pulse in either first or last appearances at 2.5 Ma or between 2.8 and 2.5 Ma. Instead, turnover in this interval was unremarkable, and mammalian lineages displayed a prolonged period of turnover especially between 2.5 and 1.8 Ma. Moreover, a combination of xeric and mesic species was found to persist from 3 to 2 Ma. Behrensmeyer et al. (1997) argued that a complex vegetation mosaic coupled with wide fluctuation over time would explain both the persistence of species of diverse ecological tolerances and the prolonged period of turnover. Whether similar results might apply to the whole of Africa has yet to be determined.

Adaptive evolution in hominins

Although the turnover pulse idea has attracted much attention, environmental hypotheses pertaining to adaptive change remain poorly developed. Hypotheses of this type differ from turnover models. They attempt to describe how environmental context impinged on survival and natural selection and in turn influenced the emergence of key adaptations. Since adaptive change may be only loosely coupled to speciation (Eldredge, 1989), these hypotheses do not necessarily relate directly to the pattern of species turnover.

Habitat-specific hypotheses. The most prominent narratives of hominin adaptive evolution are habitat-specific. Each of these scenarios points to a particular type of environment and sets forth the reason certain

adaptations arose to meet the special demands of that setting. Some scenarios simply name the particular type of habitat in which hominins were assumed to live (e.g., the savanna), while others may specify a particular direction of environmental change (e.g., the onset of dry or cold conditions). In both cases, it is implicit that natural selection had a consistent effect over time (i.e., directional selection). This process served to improve adaptive opportunities and favored certain innovations as ways of solving the challenges posed by the special habitat or trend.

The discovery of human fossils and artifacts with ice-age fauna and strata, for example, led to the idea that advances in human evolution were forged in the harsh settings of Pleistocene Europe. This view may be termed the ice-age hypothesis. An updated version of this view is as follows: cool steppe and cold periglacial conditions in mid-latitude Eurasia posed a very challenging environment to early human populations, and advances in hominid social and cognitive abilities helped to solve these problems of survival. Accordingly, the onset of ice-age habitats (due to global cooling) resulted in the evolution of key human adaptations.

As already noted, the savanna hypothesis is another habitat-specific standard and has dominated thinking about the earliest phases of hominin evolution. According to this idea, adaptation to drier and increasingly open environments was the hallmark of hominin evolution from late Miocene through at least the early Pleistocene. Savanna was the context that incited the emergence of fundamental human traits—terrestrial bipedality, larger brains, stone toolmaking, meat-eating, and associated foraging behaviors such as hunting. Essentially all textbooks prior to 1996 explained the origin of these traits in terms of adaptation to relatively open savanna, defined by the presence of grass, discontinuous trees, overall aridity, and seasonal rainfall (e.g., Klein, 1989; Wolpoff, 1980).

Recent support for the savanna hypothesis has risen from the ranks of paleoclimatologists and paleontologists (Table 2). The shared view is that emergence of dry, open

TABLE 2. Recent advocates of the savanna hypothesis

Who	What and when	Result
Vrba	Pulses of savanna expansion →	Turnover (in <i>Homo</i> and robust australopiths)
S. Stanley	↑	Novel adaptations to open conditions
G. Denton	Aridification	(e.g., terrestriality, stone tool-making)
M. Prentice	↑	
	Global cooling (~5.0, 3.0, 2.8 to 2.4, 1.7, and 1.0 Ma)	

savanna was caused by steplike episodes of global cooling starting in the late Miocene. Vrba (1995b:406), for example, refers to the onset of “the massive overall cooling trend” of the late Pliocene. Intense global cooling led to pulses of aridification in Africa, which caused savanna expansion. The shift from dense woodland to savanna had a strong effect on adaptive characteristics, including bipedality in early *Australopithecus*, hypertrophy of the chewing apparatus in *Paranthropus*, and various developments in *Homo*, such as encephalization and dependence on toolmaking (Stanley, 1992; deMenocal, 1995; Prentice and Denton, 1988; Vrba et al., 1989; Vrba, 1988).

Although the savanna hypothesis has gained recent support, it has also been strongly contested. Some authorities advocate a contradictory model—the woodland/forest hypothesis—which argues for the importance of closed vegetation in early hominin evolution. Early australopiths, according to some interpretations, were closely associated with wooded environments, exhibited significant arboreal activity, and should be considered adapted to closed habitats (Clarke and Tobias, 1995; Berger and Tobias, 1996). Fossil pollen from Makapansgat, for example, suggests that *A. africanus* inhabited conditions approximating a tropical forest (Rayner et al., 1993). At Aramis, the oldest known hominin, *Ardipithecus ramidus*, is associated with evidence of a relatively tree-dominated setting (WoldeGabriel et al., 1994). Stable isotope studies, moreover, show that the shift to C₄-dominated environments (open, grassy, heat-adapted vegetation) occurred later than previously thought, as late as 1.7 Ma, with little evidence of consistently open savanna until after 1.0 Ma (Cerling et al., 1991; Cerling,

1992; Kingston et al., 1994; Sikes et al., in press). This means that open grassland, a key ingredient of the savanna hypothesis, was by no means a regular feature of the East African landscape by the late Pliocene or even the early Pleistocene. Comparison of forest and open-habitat chimpanzees offers another interesting perspective. Tool use, hunting, food-sharing, greater social cooperation, and other traits usually associated with human evolution appear to be more strongly displayed by closed-habitat chimps. On this basis, Boesch-Achermann and Boesch (1994) have suggested that woodland or forest may have provided the initial setting in which hominins evolved. The savanna hypothesis has thus been criticized by primate researchers, paleontologists, and environmental scientists, many of whom favor replacing it with a woodland/forest-adaptation model.

A related idea—the riparian-woodland scavenging model—also underlines the importance of closed habitat to early humans. In the modern Serengeti, animal carcasses are found to be seasonally abundant in wooded areas near water. This observation led Blumenschine (1986, 1987; Cavallo and Blumenschine, 1989) to suggest that a scavenger niche could exist in riparian woodlands. Thus, during Oldowan times, marrow-eating toolmakers may have occupied the wooded zones near water, where they could exploit scavenging opportunities, which were far less available in open settings. The riparian-woodland model, like other versions of the woodland/forest hypothesis, supposes that woodlands offered a vital challenge or opportunity—in this case, carcasses that could be exploited with the help of stone tools—which grasslands did not.

Short-term variability hypothesis. The ideas considered thus far see adaptation as a response to the consistent challenges or tendencies posed by a specific type of habitat. According to a different type of explanation, important adaptive changes may arise in response to environmental variation. Variability hypotheses can be divided into short-term (e.g., seasonal variation) and long-term (i.e., variability selection).

The short-term perspective pays attention to variations experienced by an organism over its lifetime, especially seasonal fluctuation, disease, and change from year to year. This view, which we may call the seasonality hypothesis, places emphasis on how an organism adjusts to alternative environments during its lifetime, such as warm-cold or rainy-dry periods. Short-term variation is especially marked in certain regions, particularly savannas, higher-latitude biomes, or any other habitat prone to large moisture or temperature seasonality. Strong seasonality, furthermore, brings about interannual variation. The rainy season may be extreme in one year but fail in another; the difference between winter and summer temperature may be large in some years but much less in others.

The influence of short-term habitat variation on savanna organisms, including early humans, is discussed by Foley (1987). Foley notes that although early hominins occupied wooded-to-open savanna, the most significant aspect of this type of habitat is its marked seasonality. Driven by monthly variance in rainfall, significant shifts occur within each year in the abundance and availability of resources. Savanna organisms are adapted not to the variation per se but to the pattern of variation. It is the expected cyclicity of resources and their availability that is important (Foley, 1987). Short-term hypotheses of adaptive evolution thus underline repeatable variations, which represent regularities in the annual (or lifetime) adaptive setting of an organism.

The difference between seasonality and other hypotheses, then, can be subtle. Habitat-specific views lay stress on the ever-present, or consistent, adaptive problems in a given setting. The short-term variability idea emphasizes habitat variation that an organism is likely to experience and adapt to in every generation.

Long-term (variability selection) hypothesis. In contrast to seasonality and habitat-specific ideas is the variability selection hypothesis. According to this view, environmental variation is accentuated over the long term and plays a critical role in the adaptive process. Environmental change in-

volves large, episodic shifts in adaptive settings over many hundreds of thousands of years. As a result, a lineage of organisms may face multiple, substantial disparities in selective environment over time. This idea follows from the previously coined term *variability selection* (Potts, 1996a,b, in press a). The variability selection hypothesis thus states that certain adaptations have evolved due to large environmentally caused inconsistencies in selective conditions. This disparity in the Darwinian optimum favors the buildup of complex mechanisms for dealing with unexpected, episodic change. This process of adaptive evolution therefore enhances an organism's capacity to thrive in novel conditions.

Variability selection (VS) calls attention to the large remodeling of landscapes, vegetation, animal communities, and regional hydrology over long time frames. The long-term sum of habitat variability far exceeds seasonal or other types of variations encountered by individuals within their lifetime. This recurrent, wide-scale revision of environment can thus have an unusual impact on the adaptive properties of a lineage. The seasonality hypothesis implies that seasonal (or, more broadly, generation-scale) change can explain the emergence of adaptive flexibility. The VS hypothesis, by contrast, seeks the evolutionary cause of versatility in longer intervals of more dramatic change in an organism's survival regime.

The VS hypothesis requires that different individuals in different generations of the same lineage experience marked inconsistencies in adaptive setting. As it is magnified over time, the disparity in adaptive milieu shapes an overall selective environment that cannot be predicted from the more consistent selective environments of shorter periods. Selective disparity ultimately favors genes that build mechanisms of adaptive versatility. It promotes a process of adaptation to novelty, including settings never previously encountered. The resulting adaptations do not anticipate future conditions (a violation of natural selection theory); rather, their evolution stems from a prior history of major, periodic revision of the adaptive setting.

In VS, therefore, the selective effect is integrated over time. This sets up the situation in which habitat-specific traits end up eventual losers to features that in the past proved successful in novel surroundings. This unusual process thus improves adaptation to long-term environmental dynamics. (See Potts (in press a) for a more detailed discussion and response to challenges.)

By contrast, habitat-specific and seasonality explanations of evolution usually assume the operation of directional selection, in which the fitness results tend to be consistent over the long term. They focus on a specific setting, trend, or properties of variation that recur from generation to generation. The VS hypothesis is thus easily distinguished from both habitat-specific and seasonality hypotheses.

Test implications

Each of these hypotheses has testable implications—that is, a set of expectations regarding

- the general paleoenvironmental record of the late Cenozoic;
- the precise association of hominins and habitats;
- change in the breadth of habitats in which hominins lived;
- the context in which hominin adaptations first became apparent and continued to thrive; and
- the functions or utility of particular adaptive features and trait complexes.

Habitat-specific hypotheses. Global and regional environmental records should show that a particular type of habitat (e.g., woodland, savanna, glacial cold) was either maintained over a prolonged period or developed over time as a trend. Hominin fossils or artifacts, moreover, should be associated consistently with that particular type of past environment or at least a relatively narrow habitat range. The influence of a particular habitat type on adaptation can best be demonstrated in a situation in which alternative habitats were also present (and in which hominins were rare or absent).

The main expectation therefore is that hominins lived in and were especially attracted to a particular set of environmental

conditions. Accordingly, adaptive features should be well suited to those conditions and should have first appeared in that specific type of habitat. Functional analysis should therefore show that those features had properties (e.g., shape, size, biomechanical, behavioral, or ecological properties) that were particularly beneficial in the environment specified by the hypothesis (e.g., arid savanna, woodlands, glacial cold).

Short-term variation (seasonality) hypothesis. The main expectations of this hypothesis, distinguishing it from the others, are that 1) hominins lived in settings of high seasonality, 2) key adaptations reflect the scale of habitat variation typically faced over a lifetime, and 3) large-scale fluctuations have occurred on seasonal, decade, and century time scales during spans of major adaptive change.

Short-term variation may be quite extreme. According to climatologists Crowley and North (1991:11), "the seasonal cycle is the largest climate change we know of—the change in temperatures over North America from winter to summer is far greater than glacial-interglacial changes in mean annual temperatures of the Pleistocene." By this reasoning, seasonal cycles represent the widest range of environmental change to which organisms adapt in both temperate (Calvin 1996) and tropical latitudes (Foley 1987).

Greenland ice-core records further indicate that huge deviations in climate may occur abruptly on a decade-to-century time scale—thus within the lifetimes of humans and other long-lived organisms. It is possible that such rapid oscillation—and dramatic shifts on an even shorter cycle, such as El Niño—characterized the period of human evolution (Calvin, 1996).⁶ Thus, short-term variation can account for the range of settings to which hominins had to adapt. Accordingly, large interannual variations in high seasonality regions should dominate the environmental record of hominin evolution.

Variability selection hypothesis. The VS hypothesis suggests a series of well-defined

observations that differentiate it from other hypotheses. Long-term global and regional records should show large-scale environmental fluctuation. The degree of environmental change should become larger over long time periods, greatly exceeding the scale of seasonal or lifetime fluctuation. The emergence of key hominin adaptations, moreover, should coincide with spans of enhanced environmental fluctuation. In addition, these adaptations should promote versatile behaviors and responsiveness to habitat diversity and change.

The VS hypothesis also implies a set of expected observations regarding hominin-environment associations in the geologic record. These expectations are best presented in a comparison with habitat-specific explanations, as summarized in Table 3.

Comparison of these two sets of expectations leads to an important point. Paleoclimate records clearly demonstrate that dramatic environmental oscillation occurred over the past 6 million years (Figs. 2–4), a finding that appears to support the VS hypothesis. Change does not mean, however, that the selective environment of hominins (or other organisms) was similarly altered. A given species may track the geographic shifting of key resources as its environment is modified. In this way, an organism can stabilize its selective milieu rather than adapt to novel variations.⁷ Thus, the external environment (such as climate) and the selective environment of an organism may sometimes vary independently (Brandon, 1990). For this reason, habitat-specific explanations of hominin evolution are quite plausible, for they imply that early human populations continued to exploit certain favored habitats despite overall shifts in global and regional environment (Table 3, expectation 1). Alternatively, hominins may have mainly been affected by the overall trend, the average change in environment, and the trend was a more important selective factor on hominins than the variance (range and pace of fluctuation) (Table 3, expectation 2).

⁶The El Niño cycle, however, may be only 5,000 years old (Sandweiss et al., 1996).

⁷Conversely, change in an organism's selective environment (e.g., competitors, predators, disease vectors) may occur independent of climate, tectonics, or other geologic factors that alter habitats.

TABLE 3. Test expectations concerning the geologic association between hominins and paleoenvironments: Habitat-specific versus variability selection hypotheses

Habitat-specific hypotheses		Variability selection hypothesis	
Expectation 1	Over long periods, hominins were tied to a specific habitat type—for example, open savanna (savanna hypothesis), relatively closed habitat (woodland/forest hypothesis), cold steppe or periglacial setting (ice-age hypothesis)	Expectation 4	The oldest hominins occupied a diverse array of habitats (responsible for the emergence of initial adaptations); over time, hominins occupied an ever-wider diversity of environments as they evolved new means of adaptive versatility (correlated with widening environmental extremes manifested over the long term)
Expectation 2	Over long periods, hominins became associated with a new type of habitat (i.e., habitat use changed in a specific direction following the environmental trend of the period) (e.g., increasing hominin presence in open conditions supports the savanna hypothesis, even if earlier hominins were in woodland settings)	Expectation 5	Early in time, habitat use by hominins focused on a specific vegetational setting (or other well-defined environment) but became more diverse later on as the range of environmental fluctuation increased
Expectation 3	In a given stratigraphic interval (within a basin), hominins are correlated with a specific habitat type (requires demonstrating the contemporaneity of different habitat types); over time, this hominin-habitat correlation was either maintained or permanently shifted to a new habitat type	Expectation 6	In any given stratigraphic interval, hominins are found in a specific environmental setting; but in a long stratigraphic section (over long periods of habitat change), the sum total of hominin environments is highly diverse (i.e., hominins persisted through widely fluctuating environments within a locality)

The VS hypothesis differs here. It claims that external variance strongly impacted the selective environment of hominins. It asserts that variable conditions created a wide disparity in adaptive settings over time. This disparity then created an overall selective environment that fostered adaptive change in hominins via the process of variability selection.

The most important factor in testing these expectations or any environmental hypothesis is the detail and precision of data related to paleoenvironments and their association with hominins (fossils or artifacts). With this in mind, I turn to four time intervals in which evidence of hominins and/or paleoenvironments is reasonably detailed in certain localities or regions, sufficient at least for an initial test of the hypotheses defined here.

ENVIRONMENTAL RECORDS AT EARLY HUMAN LOCALITIES

6.0 to 2.5 million years ago

Eastern and southern Africa. Table 4 summarizes environmental reconstructions of ten hominin localities older than 2.5 Ma. These represent the likely contexts of early australopiths. A diversity of species, however, inhabited these locales: in eastern Af-

rica, *Ardipithecus ramidus* (Aramis), *Australopithecus anamensis* (Kanapoi, Turkana), and *Au. afarensis* (Hadar, Laetoli, Turkana); and in southern Africa, *Au. africanus* (Makapansgat, Sterkfontein). Specimens sometimes attributed to the Hominini are known from Lothagam and Tugen Hills (Hill and Ward, 1988) but lack diagnostic characters related to bipedality or canine reduction. No hominins have yet been recovered from late Miocene and early Pliocene beds at Kanam (Kanam and Homa Formations), though new work provides an outline of the environmental sequence there. Taking all the localities into consideration, Table 4 shows that no single environmental reconstruction applies to the oldest recognized members of the hominin clade or to the geographic regions where they have been found.

Kanapoi, Tugen Hills, Lothagam, Aramis, and Kanam possess sediments between 6 and 4 million years old. Large mammals and isotopic data from Kanapoi, Tugen Hills, and Lothagam suggest that a mosaic of open and closed vegetation typified East Africa during this interval and that a relatively stable mosaic might have persisted for a long time. According to Kingston et al. (1994), a heterogeneous setting composed of a mix

TABLE 4. African environments from late Miocene to Pliocene, prior to 2.5 million years ago

Locality	Age (Ma)	Interpretation	Hypothesis (conditions of early bipedality)	References ¹
Sterkfontein	3.5 to 2.5	Closed vegetation	Climbing adaptation (forest)	1, 2
Makapansgat	3.3 to 3.0	Many competing views		
		Fossil mammals and arthropods	Savanna, woodlands, or forest	3–7
		Pollen: forest/bush → grass/shrub	Fluctuation	8
		Pollen: forest (earliest australopiths)	Adaptation to forest	9
Omo-Turkana	4.0 to 2.5	Dramatic floral change in gallery forest	Forest mosaic or fluctuation	10–13
		Dry to wooded savanna plus gallery forest	Adaptation to the mosaic	14
Hadar	3.9 to 3.0	Forest/bush → open country → grassy/plain → forest/bush	Fluctuation	15–17
Laetoli	3.8 to 3.5	Open savanna with seasonal aridity	Adaptation to savanna	18–21
		Woodlands and wooded savanna	Adaptation to woodland	22
Kanapoi	4.2 to 4.0	Mixed vegetation	Adaptation to the mosaic	23
		Dry, open vegetation (micromammals)	Adaptation to savanna	24
Aramis	4.4	Forest-woodland	Adaptation to forest	25
Tugen Hills	5.0 to 2.5	Mixed grassy woodland	Adaptation to the mosaic	26
Kanam	6.1 to 3.5	Closed → open → closed vegetation	Fluctuation	27
Lothagam	7.9 to 4.7	Mixed open woodland	Adaptation to the mosaic	28, 29

¹ References: 1, Clarke and Tobias, 1995; 2, Berger and Tobias, 1996; 3, deGraff, 1960; 4, Cooke, 1978; 5, Kitching, 1980; 6, Vrba, 1988; 7, Reed, 1997; 8, Cadman and Rayner, 1989; 9, Rayner et al., 1993; 10, Bonnefille and DeChamps, 1983; 11, Bonnefille, 1984; 12, Bonnefille and Letouzey, 1976; 13, Williamson, 1985; 14, Brown, 1981; 15, Johanson et al., 1982; 16, Gray, 1980; 17, Bonnefille, 1995; 18, Hay, 1981; 19, Hay, 1987; 20, Leakey and Harris, 1987; 21, Bonnefille and Rioulet, 1987; 22, Andrews, 1989; 23, Leakey et al., 1995; 24, Winkler, 1995; 25, WoldeGabriel et al., 1994; 26, Kingston et al., 1994; 27, Potts et al., 1997; 28, Leakey et al., 1996; 29, Harris and Cerling, 1995.

of C₃ and C₄ plants prevailed in central Kenya over the past 15.5 myr. These data suggest long-term environmental stability, and that spatial habitat diversity (rather than long-term fluctuation) played a strong role in the origin of bipedality.

With regard to Kanapoi (4.2 to 4.0 Ma), Leakey et al. (1995) similarly suggest that the oldest known bipeds inhabited a spatial mosaic of vegetation. Interpretation of the mammal microfauna, however, suggests that Kanapoi's environment was open and relatively dry around 4 Ma. Although trees were present, extensively wooded tracks did not apparently occur (Winkler, 1995).

The bovid, elephant, and equid fauna from Lothagam (7.9 to 4.7 Ma) supports the mosaic interpretation. The fossils suggest a mixture of riverine forest, woodland, and open grassy patches, although the assemblage is time-averaged over a lengthy period, making it difficult to discern the variance between stratigraphic units. Stable isotopic study of soil carbonates also implies a mixed habitat at Lothagam, a prevalence of C₃ plants but with C₄ grasses also present (Leakey et al., 1996; Harris and Cerling, 1995).

At Kanam (6.12–3.5 Ma), fossil vertebrates relate to a diverse, spatially mosaic environment. Isotopic data plotted with fine

stratigraphic resolution give evidence of a temporal oscillation between 30 and 70% C₄ grasses. The data suggest a mixed C₃/C₄ plant community but with nonoverlapping variations through time (Potts et al., 1997). Since hominin fossils have yet to be found in this sequence, it is unclear whether bipeds ever encountered the range of habitat change implied by the isotopic data.

At the Ethiopian site of Aramis (4.4 Ma), fossil wood, abundant seeds of the woodland/forest-dwelling *Canthium*, and the mix of fossil vertebrates (rich in primates and tragelaphine bovids) all point to a more closed habitat (woodland or forest) than is generally recognized at the Kenyan sites (WoldeGabriel et al., 1994). The paleobotanical evidence, which seems particularly important, derives from a carbonate horizon just beneath the pedogenically altered silts that contain *Ardipithecus ramidus* and other fossil vertebrates.

Later, at Laetoli (3.8 to 3.5 Ma), the geologic clues (aeolian tuffs, calcite-rich soils, soil-weathering products) largely point to a dry savanna, where vegetation was at least seasonally insufficient to prevent wind transport of sand-sized ash particles (Hay, 1981, 1987). Interpretation of the fossil pollen samples agrees with this open savanna-grassland interpretation (Bonnefille and Ri-

ollet, 1987). However, a different reading of the evidence, largely the faunal remains, suggests a more closed, wooded community of mammals, similar to woodland habitats of the Serengeti region today (Andrews, 1989).

Around the same time, 4 to 3 million years ago, Hadar and the Omo-Turkana basin offer evidence of a diverse range of habitats. Stratigraphic analysis of fossil wood, fruit, and pollen (Bonnefille, 1984, 1995; Williamson, 1985) and large mammals (Gray, 1980; Johanson et al., 1982) suggest that considerable fluctuation in climate, vegetation, and available water sources (basin hydrology) occurred over the long term in these areas without clear sign of an aridity trend.

The wide range of environmental interpretations of Pliocene sites, both in eastern and southern Africa (Table 4), depends on the type of geologic evidence, time period, and even the taxonomic group of fossil animals and plants that are assessed in one study or another. This range includes apparent support for a savanna interpretation and for its antithesis, in which tropical forest or woodland is considered the favored environment of early bipeds. At Makapansgat, for example, pollen data examined by Rayner et al. (1993) suggest that *A. africanus* was adapted specifically to forested habitat. Yet an earlier study of fossil pollen from this same site emphasized the "fluctuating climatic and vegetational conditions" in which this species lived (Cadman and Rayner, 1989: 112).

Discussion. Late Miocene and early Pliocene environments in Africa provided the context of the oldest bipedal apes. Information about these environments is ultimately pertinent to the origin of bipedality itself. This issue continues to be one of the most problematic in the study of hominin evolution.

The largest problem in testing environmental hypotheses with data from these localities concerns the poor connection between hominin fossils and paleoenvironments. Linkage in time and space between these two types of data is imprecise. Rarely do samples for paleoenvironmental analysis come from the exact loci and sedimentary environment in which hominin fossils were

originally buried or, based on taphonomic analysis, in which the hominins may actually have lived and died. At a locality like Makapansgat, paleoenvironmental data may come from the same stratigraphic member as fossils of *Australopithecus*, but the amount of time-averaging represented by any member may be very long. Analysis of a single stratigraphic unit may yield an average environment largely irrelevant to the actual environments (and their variance) encountered by early humans. At Laetoli, surface collecting of nearly all of the fossils means that 300,000 years of fossil animals are treated as if they reflect a single community or environment. Arguments about the best or most accurate reconstruction of the Laetoli paleoenvironment are useless without better stratigraphic and analytical control over the data. This same problem applies to Hadar, Kanapoi, Tugen Hills, and most localities.

The evidence reviewed here nonetheless suggests a preliminary interpretation. The body of data does not consistently favor either the savanna or forest adaptation model, even though data from individual localities or stratigraphic levels have been used to defend both interpretations. The presence of *Ar. ramidus* in closed vegetation (at Aramis) coupled with *Au. afarensis* in more open settings later in time (at Hadar and Laetoli) might suggest that the latter evolved the capability of inhabiting more open environments, while *Ardipithecus* was confined to closed woodlands (WoldeGabriel et al., 1994). This interpretation would favor the savanna hypothesis (Table 3, expectation 2). This view can be valid, however, only if eventually more than one *Ar. ramidus* locality is found and closed habitat is determined to have been the domain of other populations of this species.

The combined evidence from all localities indicates that in general the oldest hominins were associated with a diverse range of habitats—forest, woodland, open savanna, and mosaic habitats. Lacking stratigraphic resolution in most of these sequences, it is still evident that hominins experienced a wide range of adaptive conditions at different sites and at different times. Notwithstanding the comparison between Aramis

and Hadar/Laetoli, there does not seem to be a dominant environmental trend in the data. At some sites, there are hints of long-term fluctuation in vegetation and climate. Combining all the localities also seems to support this idea on a broad regional scale.

Hence, I have argued previously that early hominin bipedality may best be explained as a response to variability selection (Potts, 1996a,b, in press a). Beyond the terrestrial evidence, the deep-sea isotopic record shows a dramatic rise in global environmental variability between 6 and 5 Ma relative to the variability in each 1 million year interval back to 27 Ma (Potts, in press a) (see Fig. 2B). The rise is enhanced even more between 4 and 3 Ma. As Table 4 shows, habitat reconstructions are also sufficiently varied to be consistent with a rise in environmental fluctuation, essential to the VS hypothesis.

The key to this interpretation, though, rests on the original functions of bipedal behavior over the period of its origin. Of what use was australopith bipedality in the environments in which it evolved and was later maintained? Based on utility, it makes sense that a novel form of terrestrial locomotion arose during forest reduction and savanna expansion. The function of early australopith locomotor structure has, however, been controversial. According to one camp, early bipeds were committed to terrestrial bipedality; their skeletal structure was designed to conduct this form of locomotion effectively (e.g., Lovejoy et al., 1973; Latimer and Lovejoy, 1990; Ohman et al., 1997). According to the other camp, the overall skeletal structure of Pliocene hominins indicates the importance of arboreal activity. Terrestrial bipedality was not particularly effective, and the behavior of these hominins was largely geared to life in the trees (e.g., Stern and Susman, 1983; Susman and Stern, 1991). The debate largely centers, then, on the degree to which early australopiths were committed to either arboreal climbing or terrestrial bipedal striding.

That this controversy persists, however, suggests a different adaptive explanation. The two viewpoints can be reconciled to a certain degree by challenging the either/or question. Environmental fluctuation led, at different times and places, to settings with

dense stands of trees and larger tracts of open vegetation. Responsiveness to this type of environmental disparity was, over time, a vital aspect of locomotor function. The locomotor system of the earliest hominins, by this interpretation, enabled them to accommodate to the habitat variance. The original functional benefit of bipedality resided in the versatility it afforded as local, prehomino populations faced a changing series of vegetation types over time. As a result, the early australopiths possessed a locomotor system that persisted for 2 million years or more, adaptable to the diverse settings that arose in the hominin geographic range between 6 and 2.5 Ma.

In brief, expectations 1 and 3 (Table 3) concerning a habitat-specific interpretation seem to be contradicted even by the poor-resolution data available. Temporal and spatial resolution of hominin-environment associations is too poor either to support or reject expectation 2 (Table 3). The savanna hypothesis (as an explanation of bipedality) would be favored if it could be shown, eventually, that 1) prehomins tended to occupy relatively closed vegetation, 2) the earliest hominins tended to live (and die) in less closed vegetation and, later still, in fairly open habitats, and 3) locomotor and positional functions of early australopiths were (in contrast to the argument above) largely dedicated to terrestrial two-legged walking.

The VS hypothesis, by contrast, does not appear to be contradicted by any aspect of the evidence. However, the sample size of sites, the resolution of time, and the precision of fossil-environment associations are not adequate to test this hypothesis effectively. The oldest bipeds may have inhabited a wide range of habitats (Table 3, expectation 4). In any one time or place, they may have occupied a fairly specific habitat which varied according to the available vegetation (Table 3, expectation 6). The data, though, do not appear to support expectation 5 (Table 3), the expansion of habitat diversity over time.

Despite global and some local evidence of fluctuation, it is quite conceivable that a mosaic of open and closed vegetation (promoted by seasonal variation) favored the origin of bipedality, including a mixture of

terrestrial and arboreal activities in early Pliocene hominins. The key question here concerns the stability of the open/closed mosaic over time. Was the mosaic itself adequate to account for the range of environments to which early Pliocene hominins were adapted? Or was a more extensive range of variability, expressed over longer time periods, crucial to the evolutionary process? This, of course, is not necessarily an either/or issue, as both spatial and temporal variability may have played important roles. The existing data from the 6 to 2.5 Ma time span, however, do not appear to imply habitat stability.

2.3 to 1.7 million years ago

Turkana and Olduvai basins. Dominated by fluvial settings for most of its history, the Turkana basin offers a rich dataset for assessing environmental change associated with early humans of the latest Pliocene. In this period, Turkana (including the Omo region) underwent a series of major paleogeographic changes (Feibel, 1988; Feibel et al., 1991; Brown and Feibel, 1991). During the same time, hominin toolmakers considerably altered their landscape interactions. This is evident in the archeological record from the growing diversity of paleoenvironments in which stone tools were discarded (Rogers et al., 1994).

About 2.3 Ma, a large, meandering river, like the Omo today, occupied the axis of the basin. The river was fed by braided streams that descended from the eastern and western highlands. Archeological sites, which consisted of low-density artifact clusters, were focused where the braided and main river systems met. Proximity to both aspects of the fluvial system was apparently critical in inducing hominins to produce and deposit stone tools. Rocks, which were obtained from the braided, marginal drainages, need not have been transported by toolmakers any great distance, as stream conglomerates were available within several tens of meters up to a few kilometers from the artifact sites (e.g., Lokalalei site: Kibunjia, 1994).

By about 1.9 Ma, the landscape had changed dramatically. The center of the Turkana basin was occupied by a sizable yet fluctuating lake fed from the north by the

proto-Omo River. Artifact concentrations were as low as before, and the choice of raw material was still quite localized, with transport distances possibly much less than 25 km (Rogers et al., 1994). The main difference is that archeological sites were stationed in at least three different contexts. One setting, most similar to earlier times, was at the intersection between braided and axial drainages. The main river itself, some distance from the braided tributaries, was used as a second setting; unlike the earlier period, the proto-Omo river itself was apparently a useful source of lithic raw material. The third setting occurred at the lake margin, where alluvial fans from the western highlands drained into the lake. According to Rogers et al. (1994), archeological remains in this context are the only known Plio-Pleistocene lake-margin sites in the Turkana basin. The fluctuating lake persisted to about 1.7 Ma (Brown and Feibel, 1991). Within the interval 1.8 to 1.7 Ma, a major shift in the isotopic composition of paleosols has been noted, which signifies a likely expansion of open C₄ plant habitat within the Turkana basin (Cerling et al., 1988; Cerling, 1992). This vegetation shift is recorded at the top of the Olduvai geomagnetic subchron, currently estimated to be 1.757 Ma (Cande and Kent, 1992).

By 1.7 Ma, another major paleogeographic shift had occurred. The central lake disappeared, replaced by an unstable fluvial system. A very dynamic series of landscapes ensued. Environments dominated by an axial river alternated with others consisting of intricate expanses of braided streams. This pattern of fluctuation, filling in of channels, followed by further carving of the floodplains, was influenced by massive volcanic activity in the region. Dramatic change occurred as volcanic ash blanketed the terrain occupied by toolmakers. Archeological sites occur in channel, gravel bar, overbank, and floodplain settings—a far greater diversity than in any earlier period, which seems to follow from the temporal fluctuation and greater spatial division of the landscape (Rogers et al., 1994).

The Olduvai basin offers a second important dataset for the latest Pliocene. During this period, the basin was lake-dominated;

many archeological remains are preserved in lake-margin settings, a point of considerable contrast to Turkana. The sediments of Bed I and lower Bed II at Olduvai (Fig. 6) are considered to span perhaps 50–100 kyr, bracketed between dates of 1.9 and 1.7 Ma (Hay, 1976a; Walter et al., 1991). A small alkaline lake (7–25 km wide) persisted throughout this time; thus, hydrological change was not as dramatic as in the longer Turkana sequence. Sedimentary, isotopic, faunal, and pollen studies nonetheless point to impressive shifts in climate and vegetation (Hay, 1976a; Cerling, 1992; Cerling and Hay, 1986; Sikes, 1994; Butler and Greenwood, 1973, 1976; Jaeger, 1976; Potts, 1988; Bonnefille and Riollet, 1980; Bonnefille, 1995).

Three significant transitions are apparent in the environmental record of Bed I and lower Bed II (Fig. 6). Wet, marshy, and wooded conditions low in Bed I (approximately 1.8 Ma) gave way to aridity and a more open setting near the top of this unit. In basal Bed II, there was a return to more moist and wooded habitats. Finally, the Lemuta Member at the top of lower Bed II signals the prevalence of dry conditions with sparse vegetation coverage. Near the end of the Olduvai geomagnetic event (approximately 1.76 to 1.75 Ma), recorded near the base of the Lemuta Member, there was a marked shift in soil $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ (Cerling and Hay, 1986). Evidently, this reflects a dramatic change in the percentage of C_4 plants—from 20–40% up to 60–80%, representing an open, grassy environment. This shift may be correlated with the similar one at Turkana (Cerling, 1992). The aridity conditions of the Lemuta Member are estimated to have lasted perhaps 50 kyr (Hay, 1976a).

Stone tool sites—both concentrations and scatters of artifacts—occur throughout the sequence. This suggests that Oldowan toolmakers had the means to adjust to the changes they faced. Averaged over the sequence, there was one major environmental transition every 33–50 kyr, which is within the range of the 41 kyr periodicity related to orbital obliquity. Later, in upper Bed II to Bed IV times, the lacustrine system was disrupted, and numerous changes in fluvial

hydrology and terrain took place in response to tectonic and climatic influences (Hay, 1976a).

Discussion. Two important developments in this time span were the origin of *Homo ergaster* (early African *H. erectus*), apparently by 1.88 Ma,⁸ and expansion of the ranging patterns of the toolmakers. With body size and limb proportions similar to modern humans, *H. ergaster* was an endurance-oriented biped whose skeleton absorbed high mechanical stresses probably related to locomotion (Ruff et al., 1993). With the Nariokotome skeleton (KNM-WT-15000) as a guide, body shape was linear and adapted to heat stress, typical of modern humans from hot, dry, tropical areas. Since it was not well adapted to relatively closed, wet environments, *H. ergaster* may have marked a transition in the climatic adaptation of early hominins (Ruff and Walker, 1993; Ruff, 1991).

The Nariokotome skeleton (approximately 1.50–1.55 Ma) postdates the dramatic shift to an arid, hot climate signaled in the Turkana and Olduvai sequences at about 1.75 Ma. In this regard, the climate-sensitive shape of this particular individual makes sense. Stature estimates based on other fossils from Turkana further suggest that the transition to tall, linear body form (\bar{x} = 170 cm, n = 6) had occurred by 1.70 Ma, whereas individuals who lived about 1.88 Ma (represented by fossils ER 1472, 1481, and 3728) were significantly shorter (\bar{x} = 147 cm, n = 3) (Ruff and Walker, 1993). In general, then, evidence for an adaptive shift in body form is well correlated with or immediately follows evidence of a major shift to hot, open habitat.

The first appearance of *H. ergaster*, however, is perhaps 130 kyr older than this climatic event. An arid interval slightly older than the major environmental shift seems to be recorded in upper Bed I Olduvai (Fig. 6). Pollen analysis suggests that this environment supported mainly small herbaceous plants rather than trees (Bonnefille and Riollet, 1980). Yet this environment is no

⁸Based on occipital specimen KNM-ER-2598 from the KBS Member of the Koobi Fora Formation (Rightmire, 1991; Wood, 1991).

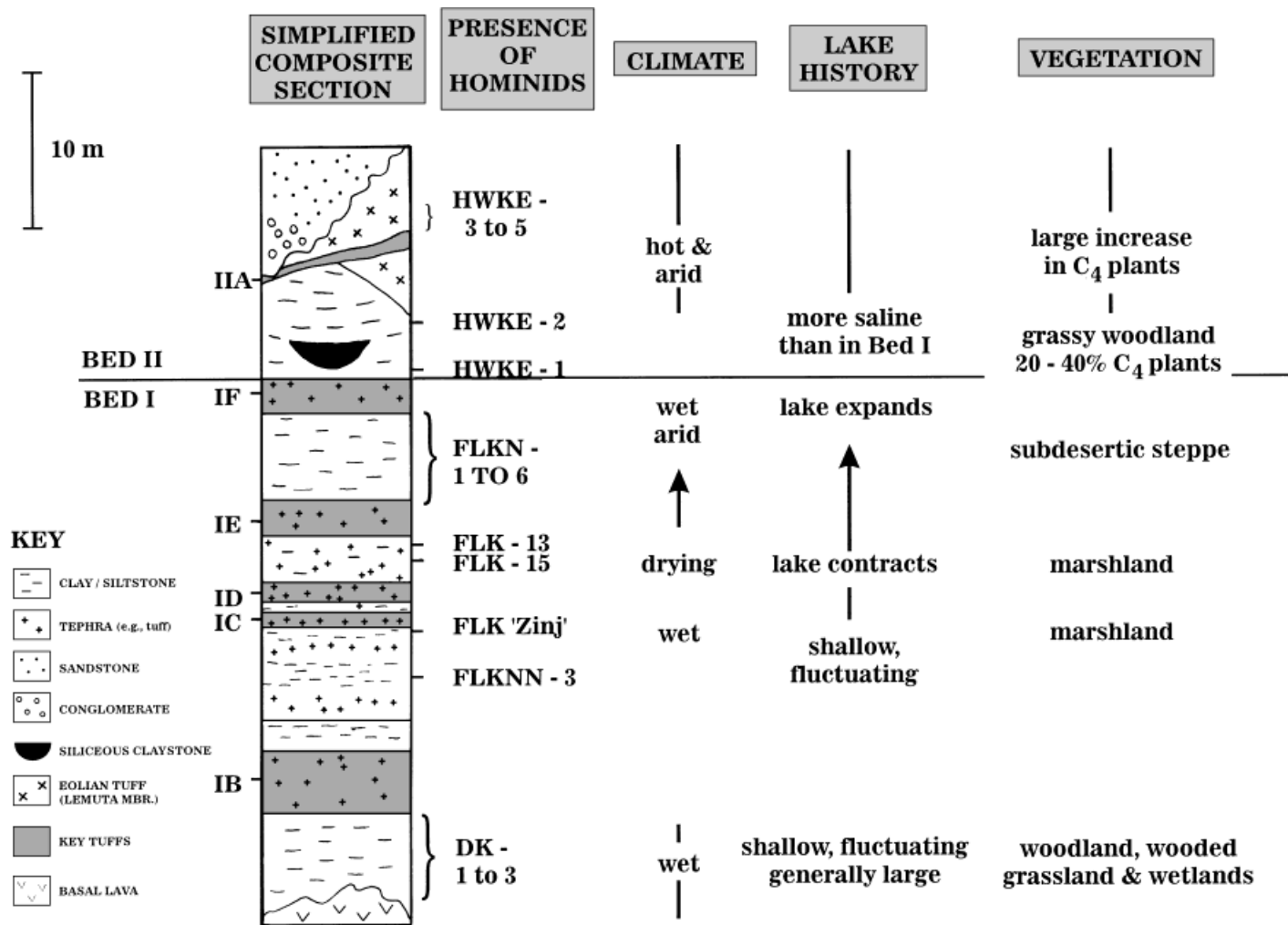


Fig. 6. Composite record of environmental change in Bed I and lower Bed II, Olduvai Gorge (northern Tanzania), approximately 1.85 to 1.75 Ma, based on interpretation of sedimentary, mineralogical, polynological, stable isotopic and faunal evidence. The presence of hominins is indicated by Oldowan archeological levels. See text for references.

older than 1.8 Ma (Walter et al., 1991), still after the first appearance datum of *H. ergaster*. One explanation is that the adaptive shift in body form was decoupled from speciation, evident also in the climatic adaptation of modern humans. If, on the other hand, further discoveries of postcranial bones indicate that body form changed in this species before 1.8 Ma, the adaptive shift preceded the most notable grassland expansion discovered so far in the East African Plio-Pleistocene record.

The second key development in the period 2.3 to 1.7 Ma is reflected by archeologically visible behaviors related to habitat use and stone transport. A significant problem here concerns the temporal and geographic overlap of potentially multiple species of toolmakers. It is not possible, except by special pleading to unsupported assumptions, to say which species was/were responsible for the stone tools deposited in any given stratum or place. Overlap of possibly three lineages of *Homo*, as well as the presence of *Paranthropus*, underscores the problem, and at present there is no obvious solution. Thus, in this period of the Plio-Pleistocene, paleoanthropologists can do no more than make observations about generic stone toolmakers—overall shifts in archeological patterns independent of how specific behaviors were apportioned to lineages. This state of affairs is less than ideal for evolutionary analysis. But observations of this sort do allow important changes in behavioral strategies to be identified, which may be correlatable with the rise of new taxa. Even when they are not correlated, generic behavioral shifts are important to identify in an analysis of hominin evolutionary history.

During the late Pliocene, Oldowan flaking was conservative. The main behavioral changes concerned the environments in which stone tools were used and left. In the Turkana and Olduvai basins, stone transport distances increased slightly, and artifacts were left in a much greater diversity of environments by the end of this period compared to its beginning (Rogers et al., 1994; Potts, in press b). In addition, the processing of animal tissues intensified. Bones from archeological sites manifest obvious damage as a result of hominins obtaining meat and

marrow from large animals (>30 kg) (e.g., Bunn and Kroll, 1986; Potts, 1988; Blumenschine, 1995; Monahan, 1996).

As noted above, these changes took place at Turkana in a dynamic series of environments. During a period of landscape instability (approximately 1.9 to 1.5 Ma), toolmakers became less tethered to local rock sources and particular habitats. They carried stones farther and made clusters of tools in more diverse areas of the landscape. The favored areas included both old and new habitats (e.g., near the axial channel and on fluvial floodplains). The evidence thus points to an expansion in landscape use rather than a directional shift.

The toolmakers of Bed I Olduvai tended to use stone sources within the confines of the lake floodplain. Transport distances rarely exceeded 3 km (Leakey, 1971; Hay, 1976a). After a series of environmental fluctuations, the toolmakers of middle Bed II expanded their range to depositional environments both within and beyond the immediate lake-margin area. Stone sources outside the lake margin were also newly exploited. These developments at Olduvai, then, parallel those in the Turkana basin.

At both localities, toolmakers were active through substantial shifts in environment and were present in arid, moist, warm, cool, more wooded, more open, lake-dominated, and fluvial-dominated phases. This suggests that Oldowan toolmakers could accommodate to periodic shifts in climate, basin hydrology, and vegetation. The persistence of hominin toolmakers and their eventual expansion into a greater range of habitats are consistent with the VS hypothesis. In this light, the transport of resources over longer distances, occupation of a wider habitat range, and intensification of animal food exploitation may represent means of dealing with large changes in the distribution of habitats, water, food, and other necessities. If this interpretation is correct, these behavioral changes can be considered adaptations to environmental instability rather than to any one specific type of habitat (e.g., woodland) or directional trend (e.g., increasingly arid savanna).

1 million to 250,000 years ago

Olorgesailie basin. Located in the rift valley of southern Kenya, Olorgesailie is a Pleistocene lake basin well known for dense accumulations of Acheulean stone bifaces (Isaac, 1977) and a well-calibrated record of fossil mammals and environmental change from about 1.2 Ma to 49 ka (Isaac, 1978; Owen and Renaut, 1981; Potts, 1989, 1994, 1996a; Deino and Potts, 1990; Tauxe et al., 1992; Potts et al., in press). The main portion of the Olorgesailie Formation, comprising 14 members, is dated between >992 ka and 493 ka, a span of about 500,000 years. The geologic sequence consists of lake diatomites, associated floodplain and fluvial sediments, and tephra.

Figure 7 depicts a composite stratigraphic section of the Olorgesailie Formation (based on observations by R.M. Shackleton, G.L. Isaac, A.K. Behrensmeyer, and R. Potts). It also indicates the stratigraphic position and relative concentration of stone artifacts as determined by recent research in the region. The illustration shows, in general terms, the periods of stability and change in the Olorgesailie basin and enables an estimate of the rate of major environmental revisions in different parts of the stratigraphic section. The datable sequence can be divided into five main intervals. Several significant changes are obvious in each interval (see Fig. 7 for details).

1. Members 1–5 (992 to 974 ka). Covering approximately 18 kyr, five major remodelings of the landscape can be documented after the lake became established (Member 1). These changes affected basinwide hydrology in ways that would have altered the distribution of water-dependent plants and animals.
2. Member 6/7 (974 to 780 ka). This part of the section records three major landscape changes. Toolmakers interacted with a series of fluvial, fluctuating lake-margin and stable, vegetated environments. From the dated pumice in Member 5 to the Brunhes/Matuyama boundary at the top of Member 7, a span of approximately 194 kyr is represented. Most of this time is taken by upper Member 7 soil formation (Potts et al., in press).

3. Members 8 and 9 (780 to 662 ka). Three major shifts in the depositional and hydrological regime of the basin are recorded in this period of about 118 kyr.
4. Members 10–12 (662 to 601 ka). In a span of 61 kyr, three dramatic environmental changes occurred involving the disappearance, reappearance, and expansion of the lake.
5. Members 13 and 14 (601 to 493 ka). In this section, covering an estimated 108 kyr, two major environmental shifts are inferred, which correspond to the two members originally recognized by Shackleton (1978).

Artifacts occur throughout the entire section. There is no consistent association between the density of stone artifacts (a partial measure of the level of hominin activity) and specific kinds of depositional environment or hydrological regime. Toolmakers did not occupy the basin continuously, but they left evidence of their activity in fluvial and lacustrine settings and at times when the lake was large, small, or not apparent at all. Analysis of paleosol stable isotopes by N. Sikes (Sikes et al., 1997, in press, and in preparation) has also documented change in vegetation, including a grass-dominated open-savanna setting in upper Member 1 and more closed, bushland conditions in later members. Overall, vegetation was more open than in the period prior to 1 Ma, as documented at other East African sites. Based on isotopic data from Olorgesailie and Olduvai, Cerling (1992) infers that grasslands became a persistent part of East African environments sometime after 1 Ma, perhaps as late as 600 ka. Even within this more open setting, extensive and recurrent alteration of hydrology and landscape features was the dominant environmental signal of the Olorgesailie Formation. Modifications occurred in episodes several thousands to tens of thousands of years apart, elicited by climatic, tectonic, and volcanological causes.

Zhoukoudian, the Loess Plateau, and Bose basin, China. Outside of Africa, hominin localities with lengthy stratigraphic records (>500,000 years) and well-cal-

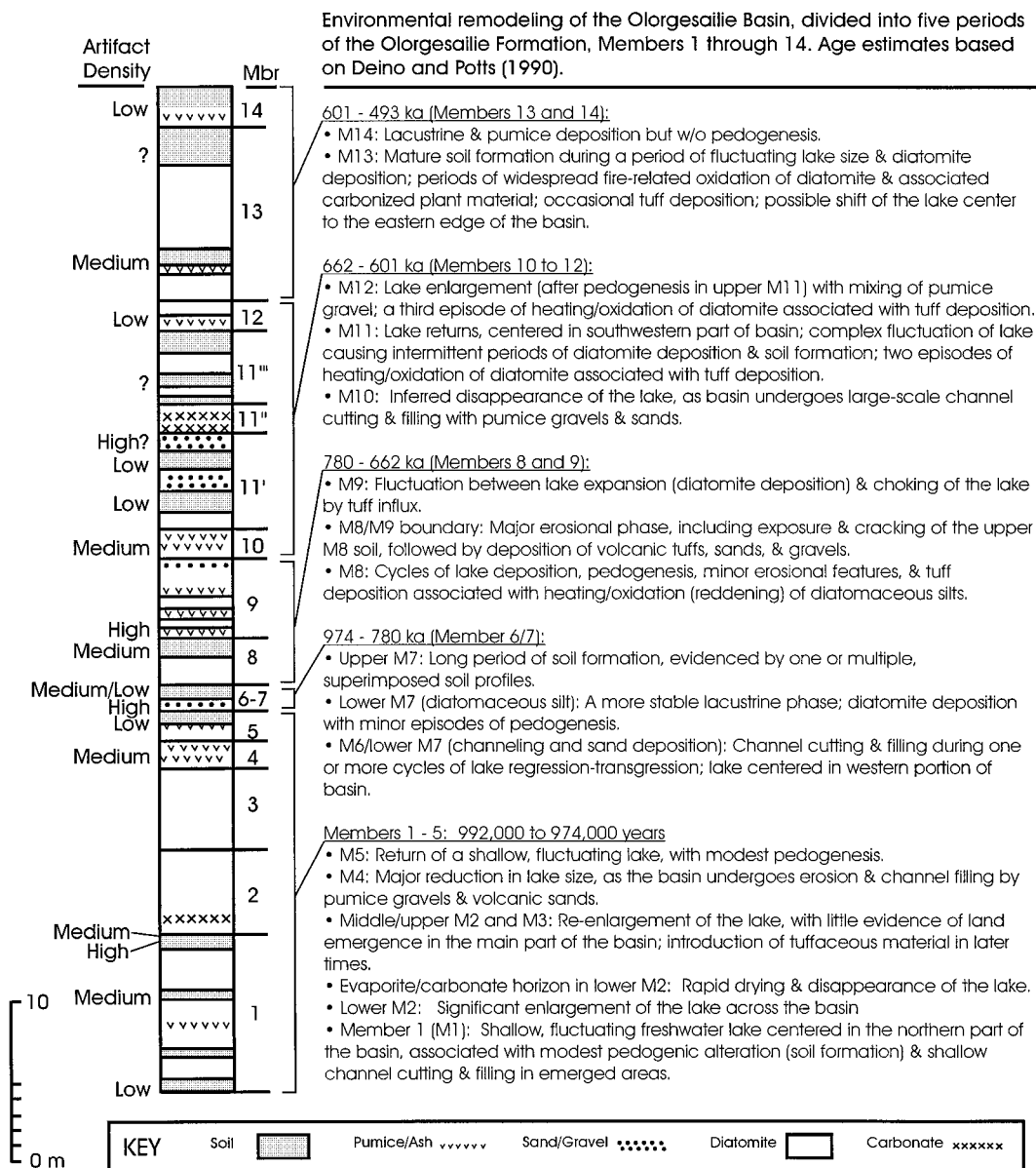


Fig. 7. Major environmental changes recorded in 14 members of the Olorgesailie Formation (southern Kenya), 992 to 493 ka, based on lithology and diatoms. The concentration of stone tools within particular strata is indicated in relative terms: high, medium, and low.

brated environmental sequences are extremely rare. One of the few that come close to meeting these two criteria is Zhoukoudian, the famed Peking Man (*Homo erectus*) cave, southwest of Beijing in northern China. A section over 40 m thick at Zhoukoudian Locality 1 has been divided into 18 strati-

graphic units, though sedimentation appears to have been largely uninterrupted. This section ranges from older than 780 ka at the base (layers 13–18) to about 230 ka (based on uranium series analysis) near the top (layers 1–3). Between 1927 and 1982, hominin fossils and stone artifacts were

recovered from layers 10 through 2, covering an estimated time range of 460 to 230 ka. *H. erectus* fossils are known from layers 2, 4, 8, and 10. Definite stone artifacts derive from layers 3–10, with the exception of layer 5 (Black et al., 1933; Jia and Huang, 1990; Binford and Ho, 1985).

A variety of views has been offered about the paleoenvironments of Zhoukoudian based on Locality 1. Mammalian fossils excavated from each layer provide a rudimentary dataset but demonstrate convincingly that substantial environmental change occurred during the period of *H. erectus*'s presence in or near the cave. According to Xu and Ouyang (1982), species that signal a cool, grassland habitat outnumber forest taxa in layers 11 and 10. Layers 9 and 8 are decidedly different: grassland rodents are absent, and forest mammals dominate the assemblage, indicating a change to a warm, humid environment. Slightly colder conditions prevailed in the time of layers 7 and 6, and a warm, humid fauna reappeared in the span of layer 5. Layer 4 contains a cold-weather mammalian fauna, with a predominance of grassland taxa. Finally, a cool, grassland-forest mosaic prevailed in layer 3 times. Xu and Ouyang (1982) consider this sequence to match up with $\delta^{18}\text{O}$ stages 12 through 8, which implies that the conditions at Zhoukoudian were affected by the phases of global cooling-warming and evaporation reflected in the deep-sea oxygen isotope curve. Based on Zhoukoudian sediments, fossil pollen, and fauna, Liu (1983) supports this idea and notes that cold-warm fluctuations intensified during the middle Pleistocene. Jia and Huang (1990), however, disagree with this conclusion. Their view of the mammalian fauna is that a single cool-warm-cool cycle is indicated between layers 11 and 1 and that in general all levels included a mixture of warm- and cool-adapted taxa. According to Jia and Huang (1990), most of the mammalian remains from Zhoukoudian belong to species that were very adaptable to climatic change.

To the south and west of Zhoukoudian is the Loess Plateau, on which thick loess deposits are distributed over an area of 274,000 km² (Liu, 1988). Although no hominin remains have, to my knowledge, been recov-

ered from the loess deposits, hominin localities such as Lantian, Dali, and Dingcun are situated in the loess region.

As reviewed earlier, China's loess sequence furnishes a record of environmental change over the past 2.4 myr. Extensive fluctuation in vegetation, moisture, and temperature characterized this region of north-central China (Fig. 4). Over the past 1 million years or so, loess accumulated uninterrupted for 40 kyr or more on at least six occasions, beginning approximately 1,020 ka, 830 ka, 650 ka, 480 ka, 180 ka, and 75 ka (Kukla and An, 1989). (According to data illustrated in Fig. 4, the earliest of these episodes may have entailed considerable fluctuation.) The loessic intervals, which represented dry, relatively treeless habitat, were interspersed with soil formation periods in which dry to moist forest prevailed.

By contrast, southern China is generally believed to have had an extremely stable Pleistocene climate. Red lateritic soils occur throughout much of this region and into Southeast Asia and India. The laterites range from a few meters to over 10 m in thickness, and their rather uniform appearance has been taken to imply a static Pleistocene environment (e.g., Teilhard de Chardin et al., 1935; Movius, 1969).

This characterization, however, appears to be incorrect. Based on recent work in the Bose basin, Guangxi Autonomous Region, an 8 m thick laterite containing stone tools (dated approximately 730 ka) exhibits strong cyclicity of clay, heavy minerals, and other sediments (possibly loess) when examined on a microstratigraphic scale (10 cm intervals) (Huang and Potts, in preparation). The Pleistocene red soils of south China, in fact, appear to have formed as part of a climatic cycle linked to the loess-paleosol cycles to the north (Zhu et al., 1995). Furthermore, analysis of fossil pollen obtained from cores drilled in the South China Sea indicates recurrent north-south migration of tropical and subtropical vegetation zones through southern China during the Quaternary (Wang et al., 1991). Together, these lines of evidence suggest that middle and late Pleistocene inhabitants of South China, like hominin populations in other parts of the world,

faced a significant range of environmental variability over time.

Discussion. Several evolutionary changes occurred in hominins over the past 1 million years. An increase in relative brain size was among the most prominent from an adaptive standpoint, and it is interesting to examine how environmental change might relate to it. Rapid encephalization in hominins occurred during the middle Pleistocene, between 780 and 130 ka (Ruff et al., 1997; Aiello and Wheeler, 1995). There is growing evidence, moreover, that cognitive and behavioral competence expanded in hominins during this same interval. This evidence may include hearths and control of fire (Kretzoi and Dobosi, 1990), manufacture of well-designed spears (Thieme, 1997), neurological control over speech (Kay et al., 1998), occupation of high latitudes (Waters et al., 1997), and possibly ways of enabling island habitation (Morwood et al., 1998). It is unclear what parts of this cognitive/behavioral package were possessed by early humans of Olorgesailie, Zhoukoudian, or central China. But as these localities offer among the best stratigraphic records for this period, they provide a way to assess the environments faced by certain hominin populations as brain size and behavior evolved.

None of these records lends support to habitat-specific explanations of hominin adaptive change. Substantial environmental shifts, local to global in scale, occurred over the past 1 million years. Large-scale changes were manifested over periods of 10^4 – 10^5 years. At Olorgesailie, 16 major revisions of basin hydrology, paleogeography, and depositional environment occurred between 992 and 493 Ma, an average of about 31 kyr between each transition. The distribution is uneven, however, with mean intervals of about 3.6, 20, 39, 54, and 65 kyr between transitions for different parts of the stratigraphic section. Since depositional rates were neither constant nor continuous (e.g., erosional phases at the base of M6/7 and M9), these estimates do not represent actual periodicities. Yet they do imply that large-scale revamping of the terrain and environment, greatly exceeding seasonal types of oscillations, took place over lengthy

periods of time. In each record examined here, long-term modifications presented a much more varied, complexly changing series of adaptive conditions at different times than any one population would have faced over seasonal or interannual periods. These points are at odds with the expectations of the seasonality and habitat-specific hypotheses and are consistent with the idea of variability selection (Potts, in press a,b).

140,000 to 50,000 Years Ago

Combe Grenal, France. The rock shelter at Combe Grenal, excavated by Bordes (Bordes et al., 1966), provides one of the longest late Pleistocene sequences in Europe and the most complete record of environmental change in southwestern France between 140 and 50 ka (Laville et al., 1980; Mellars, 1996). Nearly 13 m thick, the sediments represent the fill of a small cave, which were divided during excavation into 64 archeological layers. Figure 8 illustrates two datasets, the percentage of arboreal pollen and relative abundance of two cervid species, that serve as measures of climatic conditions. These are displayed in relation to the lithic industries deposited in the shallow cave by Middle Paleolithic toolmakers. Although Bordes (1961) believed the diversity of industries reflected different cultural traditions, others interpret the variations in terms of different activities, different phases of stone reduction, or temporal phases of a single cultural tradition. It is generally believed that populations of Neanderthals were responsible for these varied stone tool assemblages.

The Combe Grenal record documents extensive changes in environment, which are summarized by Mellars (1996).

1. Corresponding to $\delta^{18}\text{O}$ stage 6, layers 64 to 56 reflect severe glacial conditions. An extremely cold, dry, open climate is signaled by sedimentary frost cracking with little chemical weathering, large percentages of reindeer (92–97% of all ungulates [not represented in Fig. 8B]), and consistently low levels of tree pollen, most of which is pine.
2. A hiatus is then represented by heavy weathering and soil formation of earlier deposits. As no new sediments were laid

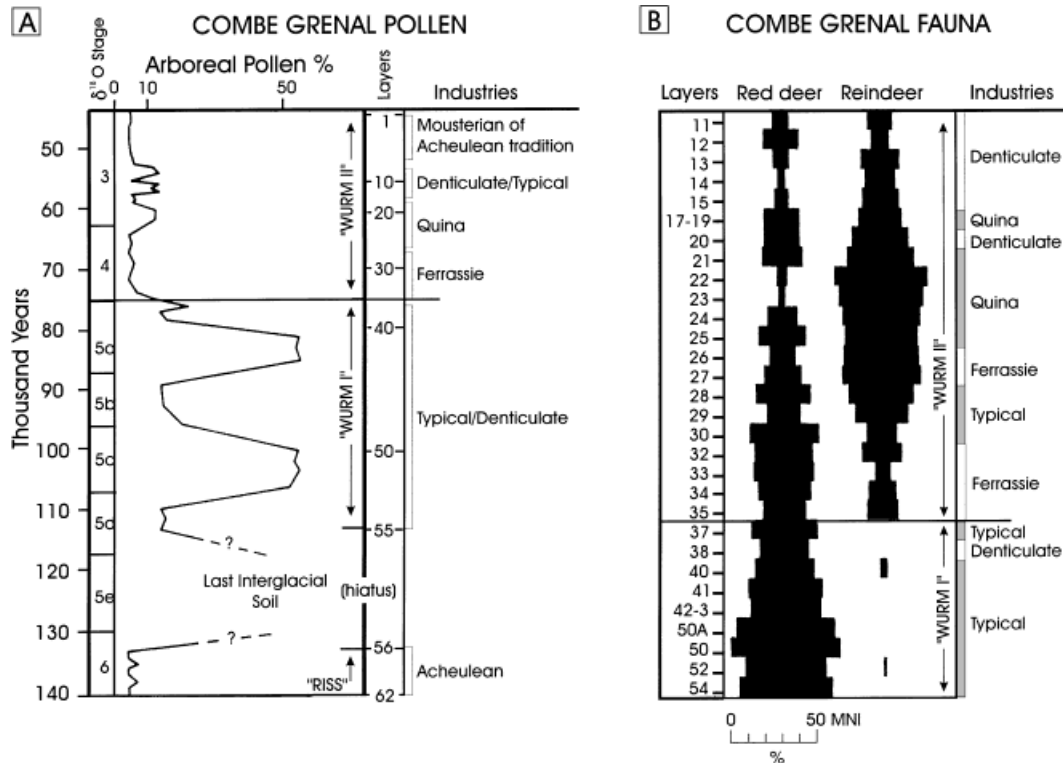


Fig. 8. **A:** Percentage of arboreal pollen in layers 1–62 at Combe Grenal (France), 140 to 50 ka, and the presence of hominins indicated by lithic industries in the same layers. **B:** Changes in the relative percentage (minimum number of individuals) of red deer and reindeer in layers 55 to 10 at Combe Grenal (approximately 115 to 55 ka) and associated lithic industries. Based on Bordes et al. (1966) and Chase (1986). (Reproduced from Mellars, 1996, with permission of the publisher.)

- down, fauna, artifacts, and pollen representing this period are absent. Correlation with the warm, humid conditions of the last interglacial, lasting for several thousand years, is thus based on the altered character of the sediments.
- Layers 55 to 38 formed during a succession of four climatic oscillations, including two severe cold episodes and two longer warm intervals. These oscillations are well portrayed in the pollen record, while the ungulate fauna shows a stable preponderance of red deer throughout. Arboreal pollen reached 60–70% during the warm times and included deciduous species like elm, lime, and alder, which require warmth, in addition to cool-loving pine and juniper. Although warm and cold phases were dramatically different from one another, at no time was there a setting comparable to the glacial periods of layers 62 to 56 and Würm II.
 - A dramatic environmental shift back to full glacial conditions, with extremely low levels of arboreal pollen (nearly total disappearance of species other than pine), is recorded from layers 37 through 1. In the continuous pollen records of eastern France, Grande Pile and Les Echets (Fig. 5), the transition to glacial conditions is marked by one or two very rapid oscillations (i.e., within 1,000–2,000 years), to warm-humid, then cold, and finally cool-wet conditions. These fluctuations may be reflected at Combe Grenal in the warm, wetter episode of layer 38 and a weathering horizon between layers 36 and 35. Following layer 35, dry, cold steppe prevailed—a markedly rigorous setting for humans inhabiting the region.

Although data are lacking for the last interglacial (hiatus), it appears that Neanderthal populations occupied the cave and its surroundings essentially during the entire sequence, leaving late Acheulean and Mousterian artifacts in all settings.

Discussion. The environmental conditions of Mousterian toolmakers in western Europe ranged from glacial steppe/tundra to interglacial temperate forests. The last interglacial period ($\delta^{18}\text{O}$ stage 5e) represented an especially warm period that contrasted starkly with intense, long-lasting glacial conditions immediately before. In the initial 5 kyr of the last interglacial, global mean annual temperature increased 10–15°C (as did local temperature) (Fig. 5), and sea level rose 5–6 m above that of the present (compared with 100 m lower during isotope stage 6). Interglacial conditions (and interstadial periods during the last glacial) established a temperate climate that included cold winters, to which trees of the European deciduous forests were adapted. Hominin populations in the vicinity of Combe Grenal, therefore, lived in either seasonally or perennially colder surroundings than populations in most other parts of the world.

Western European Neanderthals were obviously equipped to deal with large changes in vegetation, fauna, and climate, such as those documented at Combe Grenal. These hominins produced a more complex stone technology and diverse series of tool kits than their predecessors, which may have served a wider variety of special tasks. The pattern of faunal remains at Combe Grenal (Fig. 8B), moreover, is informative about foraging behavior. The shift from red deer to reindeer matches the shift from more temperate habitat (layers 55 to 37) to cold, dry conditions (layers 35 to 10). This suggests that the foragers of Combe Grenal were able to adjust to major alterations by changing their focus from a climatically tolerant yet mainly temperate species (red deer) to a cold steppe species (reindeer). The tremendous stability of red deer representation in layers 55 to 37 (approximately 115 to 75 ka), however, further implies that Mousterian toolmakers in this area also stabilized their access to certain focal resources even as

climate and vegetation varied over time. The possible strategies for accomplishing this might have involved shifting to seasonal (e.g., summer) use of the site during cold phases (isotope stages 5a and 5c), which might have enabled continued access to red deer herds, or long-distance tracking of red deer (and transport of parts back to Combe Grenal) as its range shifted in response to climatic oscillation.

Both patterns—initial stability and later change in faunal exploitation—suggest the considerable adaptability of Mousterian toolmakers at Combe Grenal. The same conclusion is warranted by the nearly continuous presence of toolmakers through a period of vast environmental alteration. As we have seen in other places and times, this body of evidence best fits the VS hypothesis (e.g., Table 3, expectation 6). The humans of Combe Grenal certainly were not tied to a single type of habitat. Nor did they appear to be more successful as the environment changed in one particular direction compared with another. Moreover, thousands to tens of thousands of years passed between major remodelings of the adaptive setting. Long-term shifting of vegetation and climate far exceeded seasonal ranges of variation. This observation conflicts with any attempt to explain the continuous presence of hominins in this region over time in terms of adaptation to seasonality.

Yet on the basis of limb-bone proportions (Trinkaus, 1981; Holliday and Falsetti, 1995) and nasal and facial morphology (Wolpoff, 1980; Coon, 1962), the skeletal structure of European Neanderthals appears to have been adapted specifically to colder environments. This body of evidence implies that Neanderthal (or ancestral) populations underwent directional selection adapting them to habitats ranging from cool to glacial cold. This view is, of course, supported by the environmental evidence from western Europe. From an adaptive perspective, then, the Neanderthals (Mousterian toolmakers of the early Würm) were an intriguing composite. They evidently had behavioral strategies that permitted them to persist through wide changes in habitat. Yet the one consistency was a relatively cold to cool temperate

(i.e., seasonally cold) climate; their bodies manifested adaptations to this regularity.

Despite evidence of behavioral adaptability, there is also evidence that Mousterian toolmakers were somewhat conservative in their responsiveness to changing circumstances. As Chase (1986) points out, for example, faunal exploitation patterns at Combe Grenal did change with climate but were slow to do so. Even though the humans at this site ultimately switched to hunting reindeer during the period beginning around layer 37, they did not do so quickly (Fig. 8B). Compared with modern humans who populated the same region later, Mousterian hunters did not specialize nearly as much by exploiting different animals when climate changed. In many Upper Paleolithic sites of the last glacial period, for example, reindeer represented up to 95–99% of the faunal remains, suggesting that hunting was more distinctly tuned to climatic conditions than evidenced at Combe Grenal. This is just one of several lines of evidence indicating that later occupants of western Europe were more responsive to environmental dynamics than the Neanderthals (Mellars, 1996).

ENVIRONMENTAL PERSPECTIVES ON ADAPTIVE CHANGE

From this review, there appears to be no single, all-encompassing environmental explanation of hominin evolution. Diverse selective processes operated on early human populations in different lineages, times, and places. In the anatomy of *Homo ergaster* and Neanderthals, for example, the results of adaptation to specific conditions are manifested: in *H. ergaster*, heat stress in an open tropical African habitat; in Neanderthals, adaptation to perennially and seasonally cold habitats in ice-age Europe and Asia. Seasonality, moreover, was a consistent part of the contexts in which hominin evolution occurred. Seasonal variations are critical to maintaining the savanna mosaic of Africa and the temperate habitats of Eurasia (e.g., deciduous forests and steppe). For this reason, it is often impossible to distinguish between evolutionary responses to specific types of habitat and to seasonal aridity or cold.

Although the recurrent opportunities and challenges of savannas, woodlands, and ice-age habitats all had an effect on adaptation, the analysis here adds a different dimension to the picture of hominin evolution. Direct study of past strata highlights the inconsistency of adaptive settings over long time frames and indicates that certain key hominin adaptations emerged during periods of intense habitat instability.

The results of this analysis can be summarized as answers to three questions:

1. *Did the origin of major hominin adaptations usually coincide with the appearance of a particular type of habitat or with a span of rising environmental variability?*

On the basis of oxygen isotope data, the past 6 million years were a time of rising environmental variability. The range of climatic fluctuation increased in successive periods. Variability continued to rise to the point that, by the middle Pleistocene, the variation in single isotopic oscillations (covering 100 kyr) usually equaled or exceeded the average change in $\delta^{18}\text{O}$ over the past 6 million years. Variability in global climate therefore swamped the overall trend toward cooling and drying. There is no doubt that environments did become colder and more arid, but reversals in the trend had arguably a more significant impact on Earth's climatic history since the late Miocene. The emergence of hominins coincided with the oldest intervals of rising variability. Complex adaptations unique to humans originated as climatic variability became magnified. Furthermore, virtually all other proxies of past environments—continental dust, pollen, and loess sequences—confirm that habitat variability increased over time in terrestrial settings.

2. *How were early humans and environments correlated over the course of hominin evolution? In regions occupied by early humans, were their remains consistently associated with a particular type of habitat, a stable mosaic of settings, or a highly fluctuating range of environments?*

All four time spans—and limited number of hominin localities—explored here manifest a high degree of habitat remodeling over time. In long stratigraphic sequences, the amount of variation greatly exceeded sea-

sonal types of variation; the tempo and kind of environmental alteration, moreover, differed qualitatively from seasonal oscillation. Evidence of hominins occurred through essentially the full diversity of paleoenvironments that ensued over time, as reflected in lengthy stratigraphic sections. This suggests that hominin populations actually encountered numerous alterations of the landscape, climate, and biota in the localities we have examined. These findings violate the expectations of habitat-specific hypotheses—expectations 1–3 (Table 3)—and the seasonality hypothesis. But they are not usually in disagreement with expectations 4 to 6 (Table 3), implied by the VS hypothesis.

The data available for most hominin localities, though, are still inadequate to fully test these three latter expectations. It is unclear, for example, whether African hominins of the early Pliocene encountered more or less habitat fluctuation than middle Pleistocene hominins. Whether a wider degree of habitat change was represented by 500 kyr at Hadar or by an equivalent time span at Olororgesailie cannot yet be answered. Thus, the available data cannot distinguish between expectations 4 and 5 (Table 3) relative to the VS hypothesis. Very few studies have attempted to address the habitat specificity of hominins within narrow stratigraphic intervals and across time (Table 3, expectation 6) (Potts et al., in press). The oxygen isotope record gives a hint that environmental diversity, although already magnified in the period between 6 and 3 Ma, was further exaggerated in successive intervals over the span of hominin evolution (Fig. 2B). It remains to be seen whether the sum of environmental records from hominin sites during this span will show the same pattern.

3. *What were the functions of key adaptations? Were they designed to best meet the regular, consistent challenges of one main type of environment or directional change or to best respond to large-scale habitat inconsistency over the long term?*

We have briefly assessed the functions of certain hominin adaptations (or adaptive trends), including bipedality, encephalization, stone tool transport, and growing cognitive sophistication. These fundamental characteristics are included in virtually every

scenario of human evolution. In each case, these features first appeared and became elaborated within very dynamic environmental sequences.

Obviously, ground bipedality makes sense in a landscape with few trees. On this logic, bipedal striding evolved as an adaptation to increasingly open settings, in line with a habitat-specific view. By studying the paleoenvironmental records of hominin sites, we find, however, that bipedal behavior emerged and was maintained over a long time in a wide variety of contexts—in relatively closed, open, mixed/mosaic, and (where sequences have sufficient time depth) fluctuating environments. This finding seems to resolve the debate about bipedal vs. arboreal competence in *A. afarensis*: namely, this and other early australopiths possessed a locomotor/positional system that enabled the combined competence of both. A single anatomical complex oriented toward versatility (climbing and walking) evolved as landscapes were remodeled over many thousands of years. If this interpretation is correct, it means that the locomotor system of the earliest hominins was adapted to the instability of late Miocene and early Pliocene habitats. Although very few records exist in Africa from the period prior to the earliest accepted australopiths, the global ocean record (e.g., Fig. 2) suggests that environmental instability was in fact on the rise during the latest Miocene.

A similar conclusion applies to other major adaptive features when analyzed in an environmental context. Enlargement of the brain relative to body size during the middle Pleistocene is a case in point. Our analysis reveals that habitats of this period underwent large revisions and that populations were subject to strong inconsistencies in selective environment. Considering the actual evidence, the view often propounded by evolutionary psychologists, who have made a large impact on the study of human cognitive evolution, needs to be reassessed. It is patently incorrect to characterize the human ancestral environment as a set of specific repetitive elements, statistical regularities, or uniform problems which the cognitive mechanisms unique to humans are designed to solve (e.g., Tooby and Cosmides, 1989,

1990, 1993; Pinker, 1994). This portrait of the Pleistocene environment should be discarded and with it the view that the human mind is composed mainly of innate special-purpose devices or algorithms tied to a particular array of past adaptive possibilities (Potts, in press a).

A variability-selection perspective, by contrast, implies that the cognitive mechanisms evolved in Pleistocene humans fostered the input, analysis, and mental representation of highly varied external information and the output of versatile, novel response. The archeological record of the past 700 kyr strongly suggests that brain functions and actual behavior were designed to accommodate a diverse series of adaptive settings, also evidenced in the archives of Pleistocene environmental history.

It is unlikely that the emergence and spread of modern *H. sapiens*, in its ecological diversity, was preceded by a long process of habitat-specific adaptation. The apparent replacement of Neanderthals in western Europe by populations more tropically adapted (Trinkaus, 1981; Holliday and Falsetti, 1995) is especially significant, for it implies prior adaptation to environmental diversity on a grand scale, which yielded populations fit to accommodate to the hot tropics, the cold regions where Neanderthals had lived, and even more extreme environments. The social adaptations of these late Pleistocene humans included sophisticated means of buffering environmental uncertainty and thriving in novel settings (Potts, in press b).

To summarize, there is very little basis for thinking that adaptive settings were consistent over many generations or changed in a consistent direction during the course of hominin evolution. Habitat-specific scenarios, which have prevailed in paleoanthropology, furnish a poor framework for explaining the origin of most complex human adaptations. Short-term habitat variation also offers a limited basis on which to account for key adaptive changes. This hypothesis, as we noted earlier, relies on the claim that short-term variation, such as seasonality, was sufficiently large to have led to the adaptive flexibility observed in humans. The environmental records examined here contradict this claim. The time frame of environ-

mental variability in hominin localities was not both rapid and extreme (i.e., unlike the Greenland ice cap). Rather, variability in landscape structure, vegetation, and resources became greatly extended over spans of 10^4 – 10^5 years and involved a substantially different type and range of environmental remodeling than exhibited on a seasonal or lifetime scale. Adaptation to short-term patterns of variation does not therefore result in adaptation to the longer time frame of habitat remodeling.

As a final point, it is important to note that the episodic revision of landscapes inhabited by hominins would also have altered the social context in which individuals competed for resources. Resource restructuring and uncertainty, according to the VS hypothesis, fostered novel strategies of competition and social cooperation. Given the environmental dynamics we have discovered, there is little basis for dismissing ecological factors while embracing social competition as an explanation of cognitive evolution and behavioral complexity (contra Humphrey, 1976). The two surely went hand in hand. Indeed, the case can be made that a strongly cooperative dynamic within social groups proved highly beneficial over the long term as a means of accommodating to unexpected ecological variability.

CONCLUSIONS

Three main kinds of environmental explanation can be considered in scenarios of hominin adaptive evolution. My goal has been to present these ideas as testable hypotheses. Habitat-specific hypotheses focus on the adaptive opportunities or challenges of open savanna, densely wooded, or ice-age (cool temperate and periglacial) environments. The seasonality hypothesis emphasizes the impact of short-term environmental variation on the adaptive process. The variability selection (VS) hypothesis postulates that wide variability in adaptive settings over time ultimately favored and helped build complex adaptations which were responsive to novel conditions. Based on preliminary tests of environmental records from various hominin sites, the main findings of this review can be summarized as follows.

1. Although usually ignored in explanations of human evolution, dramatic environmental fluctuation became magnified over long periods of time and had substantial impact on adaptive evolution in hominins. According to the VS hypothesis, the functions of key adaptations and adaptive trends—Pliocene bipedality, stone tool transport and use, and Pleistocene brain enlargement—primarily served the purposes of behavioral versatility. These traits enabled ways of adapting to environmental novelty—that is, to the dynamic properties of environments, thus including settings that had not been previously encountered. The selective process that brought about such traits must have operated over broad time scales of habitat disparity.
2. Environment-specific adaptations did characterize certain lineages of hominins. These features, however, may have largely involved anatomical structures and related physiological functions rather than complex behavioral, cognitive, and social functions, which typically are central to accounts of human evolution. Habitat-specific scenarios do not adequately explain the key adaptations they were originally meant to explain. The savanna hypothesis, for example, does not seem to offer a sufficient account of the locomotor versatility that arose in early Pliocene hominins.
3. Short-term environmental variation was ubiquitous in the regions occupied by early human populations, though seasonality or generational-scale variation usually left no mark in the geologic record. A much more impressive archive of environmental fluctuation was left over spans of many thousands of years. Stratigraphic records at hominin sites show that relatively stable environmental periods were repeatedly interrupted by large shifts in climate, basin hydrology, and landscape structure. The origin of important human characteristics emerged as hominin populations confronted a widely disparate range of selective environments. In other words, the general trends of human adaptive evolution are better portrayed as a response to the dynamic (unstable) properties than to the consistent properties of environments since the late Miocene.
4. It is important to note that most organisms are tied to a narrow range of adaptive conditions—that is, they are habitat specialists. In the face of environmental fluctuations, these species were apparently sufficiently mobile or dispersed to enable geographic tracking of requisite habitats and resources. Other lineages became extinct, a frequent occurrence in most clades of Pleistocene large mammals. In still other cases, populations or species lineages became adapted over time to a growing diversity of ecological settings. These lineages underwent a process of adaptive change that decoupled them from any one specific habitat. This process seems to have occurred repeatedly in hominins over the past 5 million years (Potts, in press a).
5. Further understanding of the adaptive history of hominins requires well-calibrated data on paleoenvironments and their exact association with hominins. Tests of environmental hypotheses rest heavily on correlation. The strength of these tests depends on improved stratigraphic resolution of the fossil, artifactual, and environmental records at hominin localities. Raising the density of paleoenvironmental data will prove especially valuable. Future progress cannot rely on data solely from individual localities. Instead, comparative study of samples of hominin localities from particular time spans is required. This type of research therefore leans heavily on integrated work by teams of geologists, paleoanthropologists, environmental scientists, and geochronologists. Without this integrated approach, paleoanthropology is relegated to sketching the phylogenetic and technological outline of human evolution while missing the substance of the story, the contexts and processes of adaptive change.

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